Ecosystem Dynamics in an Extreme Environment: Hydrologic Controls on Biological Activity in Lake Fryxell, Antarctica

Research Thesis

Presented in partial fulfillment of the requirements graduation *with research distinction* in Earth Sciences in the undergraduate colleges of The Ohio State University

By

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Abstract

The McMurdo Dry Valleys of Antarctica constitute a large and significantly ice free area of Antarctica at 78 degrees south latitude. The area is a polar desert but contains several lakes fed by glacial melt water from four to twelve weeks of the year. Over the past twenty years data have been gathered on the lakes located in Taylor Valley, Antarctica as part of the McMurdo Dry Valley Long-Term Ecological Research program (MCM-LTER). All data are publically available at www.mcmlter.org. This thesis is part of a larger investigation that seeks to understand the impact of climate on the biological processes in all the ecosystems within Taylor Valley, including the lakes. These lakes are stratified, closed-basin systems and are perennially covered in ice. Each lake contains a variety of planktonic and benthic organisms that live on the edge of survival in this extreme environment.

The biological processes in these lakes are sensitive to small variations in climactic conditions. Subtle changes in these conditions can have a large impact on measures of planktonic production and planktonic biomass. Previous work has demonstrated that biological activity in the lakes is mostly driven by ice thickness because ice thickness greatly affects the input of photosynthetically active radiation (PAR). Stream water input of nutrients is also thought to be a factor in lake productivity. The work presented here focuses on Lake Fryxell, one of the three main lakes in Taylor Valley, which is fed by thirteen streams. In this thesis, a statistical approach was used to link the physical, chemical, and biological processes within the lake to the nutrient-bearing streams that flow into it. In this statistical approach stream flow data are compared to biological data to identify the association between stream flow and various biological parameters. Three conclusions were

drawn from this analysis. I then attempt to explain each of these findings through citation of previous work and the generation of new hypotheses.

Firstly, it was found that biomass parameters were more affected by input of stream water than were biological production parameters. Other studies have demonstrated that there are other factors such as photosynthetically active radiation and dissolved organic carbon that have a significant influence on production parameters. Secondly, bacterial plankton responded more quickly to input of stream water than did phytoplankton. I explain this difference by hypothesizing that the nutrients consumed by bacterial plankton move more quickly through the water column than the nutrients consumed by phytoplankton. Lastly, it was found that a direct relationship between biological parameters and the log of annual average instantaneous stream discharge was most effective at predicting biological activity. I explain this by hypothesizing that past a certain annual average instantaneous discharge, stream flow has less and less of an effect on lake ecology.

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Acknowledgements

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Introduction

The climate and geography of Taylor Valley

Taylor Valley is one of the McMurdo Dry Valleys which constitute the largest ice-free area in Antarctica. It is located at approximately seventy eight degrees South latitude. With a mean average temperature of approximately negative twenty degrees Celsius and less than ten centimeters of precipitation per year, Taylor Valley is a polar desert (Fountain et al., 1999). In Figure 1 the three large closed basin lakes located within the Valley: Lake Bonney, Lake Hoare, and Lake Fryxell are displayed. In the austral summer, temperatures can exceed zero degrees Celsius for a number of hours per day for about four to twelve weeks, and glaciers in the valley melt (Fountain et al., 1999). This glacial melt constitutes the water supply that flows into the lakes at the valley floor.

In some places the glaciers are in direct contact with the lakes. For example, a portion of Canada Glacier touches Lake Fryxell (Figure 1). Any water that enters the lake directly from this glacier is not gauged. However, the vast majority of the water that enters the lake comes from the streams that surround the lake (Fritsen et al., 1988), and most of these streams are gauged. In the case of Lake Fryxell, there are thirteen streams connecting the surrounding glaciers to the lake. All but four of these streams are gauged. Because all of these lakes are perennially ice-covered, direct interaction between the atmosphere and the lake water is limited (Lyons et al., 1998). Because of their place in a high polar latitude locality, the lakes are in perpetual darkness for half of the year. The McMurdo Dry Valley Long Term Ecological Research (MCM-LTER) program has been collecting data on the ecosystems within Taylor Valley since 1993 (www.mcmlter.org).

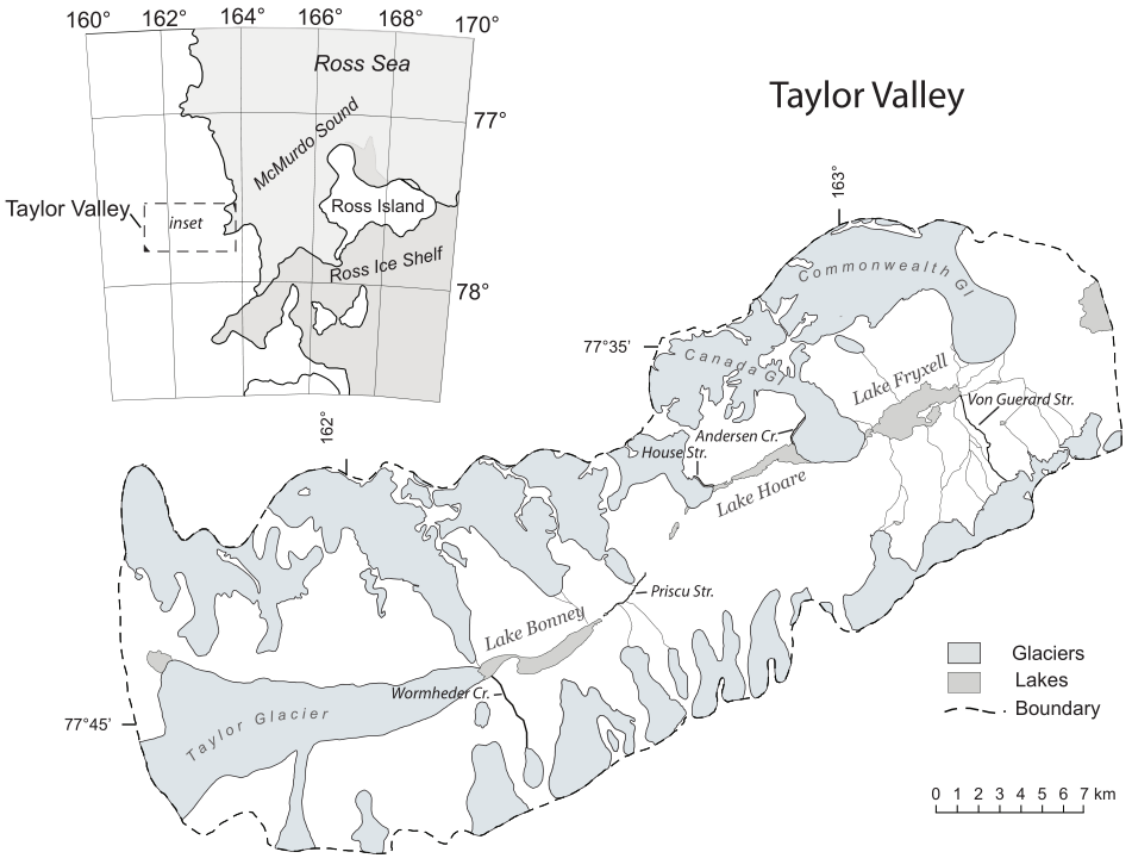

Figure 1: Map of Taylor Valley.

A Brief Introduction to the Ecology of Stable, Closed Basin Freshwater Lakes

Fluctuations in light, oxygen, carbon, nitrogen, and phosphorus heavily influence lake ecology (Moss, 1998). Lake Fryxell is a closed basin lake, with brackish salinity as a result. Lake Fryxell never overturns due to its stable temperature and extreme salinity gradient (Figures A2 and A3 in Appendix A) (Lyons et al., 1998). Due to its lack of direct connection to the atmosphere, this stratification of lake conditions is rarely disturbed. Because of this strong density gradient and water column stability, the surface waters act as a "biological pump" wherein nutrients and dissolved inorganic carbon fixed at the photic zone are later lost to the bottom waters through particle sinking (Moss, 1998). This particulate organic matter is mineralized at the bottom of the lake creating high

concentrations of CO_2 and dissolved nutrients at depth (Figures A5 – A12 in Appendix A). Most of the phytoplankton biomass in a stable lake occurs at the transition between the nutrient-rich zone extending up from the bottom of the lake, and the euphotic zone extending down from the lake's surface (Moss, 1998).

Motivation for this Research

This thesis is part of a larger investigation that seeks to understand the impact of climate variations on the biological processes in all the ecosystems within Taylor Valley. The conditions for life in this extreme environment are the product of a delicate and unusual balance of climatic conditions. These conditions result in an ecosystem in which subtle changes in physical conditions can have a large impact on biological parameters. Biological productivity in the lakes is mostly driven by ice thickness as it greatly affects the input of photosynthetically active radiation (Priscu et al., 1999). Stream water input of nutrients is also thought to be a significant factor regulating planktonic biological processes (Herbei et al.). The work presented here focuses on one of the three main lakes in Taylor Valley, Lake Fryxell. Utilizing a statistical approach I have used stream flow data combined with biological data to identify the association between stream flow and various biological parameters.

Goals and Objectives

The overall goal of this research was to investigate of the effect of climate variation on the lake ecosystem under investigation. Specifically, I asked the question: "how do variations in stream flow into Lake Fryxell affect lake ecology?" The following research objectives were addressed in this thesis:

1. With a statistical approach, determine whether stream flow into Lake Fryxell affects the biological activity within the lake. Hypothesis: Variations in stream flow have a measurable effect on lake plankton processes such as primary and bacterial production and measures of biomass such as bacterial enumeration and chlorophyll-a concentration.
2. Use the understanding gained about the influence of physical processes on Lake Fryxell and established general principles for these lake systems to generate new hypotheses that can account for statistical findings with a physical explanation.

Literature Review

Previous research by MCM-LTER members has demonstrated that light limits phytoplankton growth in the lakes in Taylor Valley (Priscu et al., 1999). Ice cover transparency is the primary factor affecting under-ice photosynthetically active radiation (PAR) in these lakes. Phytoplankton exist in very low light conditions below the photon saturation threshold much of the time, even in the austral summer (Lizotte and Priscu, 1992; Priscu et al, 1999). Therefore small fluctuations in underwater PAR can have a profound effect on photosynthetic rates in these lakes. One of the effects of changing primary production (PPR) is the case in which a decline in ice cover transparency reduces PPR which in turn limits the uptake of soluble nutrients (Priscu, 1995).

Experiments and field observations have been conducted by MCM-LTER scientists over the past twenty years for the purpose of better determining the relationship between meteorological parameters and their biological response. Herbei et al. (2010) make the first attempt to model the relationship between these two things. Herbei et al. (2010) conducted this work on Lake Hoare only, but demonstrated that fluctuations in PAR and concentration of phosphate in the water column correspond to changes in primary production rates. This suggests that phytoplankton growth in the lake is greatly affected by fluctuations in light and nutrients. Surprisingly, Herbei et al. (2010) found little relationship between organic carbon concentrations and planktonic bacterial production. This did not support the proposed hypothesis involving an ecological relationship between these two parameters.

The work presented within this thesis is a direct outgrowth of the earlier work presented in Herbei et al (2010). In this thesis a similar modeling approach was applied to

Lake Fryxell in which the in-lake biological variations were compared to the stream discharge data collected over the last twenty years of the MCM-LTER. Annual average instantaneous stream discharge is considered a surrogate for climate variability, as it is an indicator of small scale climatic variability in Taylor Valley (McKnight et al., 1999; Fountain et al., 1999). Since there are many more streams flowing into Lake Fryxell than into Lake Hoare, this approach seemed more reasonable to apply to Lake Fryxell than to Lake Hoare. In addition, because of the direct input of nutrients and heat from stream water, stream variability could greatly influence both ice cover thickness and nutrient concentration. Both the experimental work (Priscu 1995; Priscu et al., 1999) and the initial modeling results (Herbei et al., 2010) have suggested that ice cover thickness and in-lake nutrient concentrations were the primary physical drivers of in-lake biological processes.

Methods

Summary

A Long Term Ecological Research program (LTER) has functioned in Taylor Valley since 1993. Data have been gathered on physical, chemical, and biological parameters in the lakes, the streams, glaciers, lake ice, and soil. In this thesis I utilized stream discharge data from this LTER program and compared it to the LTER biological data from Lake Fryxell. Correlations were then run comparing annual average instantaneous discharge to each of the four main sets of limnological productivity and biomass data: primary production, bacterial production, chlorophyll-a concentration, and bacterial enumeration. For each biological data set a correlation was run under eight different statistical conditions described below. Biological data were compared with stream discharge data from one and two years prior. For each of those two cases, four different simple models were applied, creating a total of eight models per biological data set:

Model 1a: log(annual avg. inst. disch.) v. log(avg. of bio. data at a one year lag)
Model 1b: annual avg. inst. disch. v. log(avg. of bio. data at a one year lag)
Model 1c: log(annual avg. inst. disch.) v. avg. of bio. data at a one year lag
Model 1d: annual avg. inst. disch. v. avg. of bio. data at a one year lag
Model 2a: log(annual avg. inst. disch.) v. log(avg. of bio. data at a two year lag)
Model 2b: annual avg. inst. disch. v. log(avg. of bio. data at a two year lag)
Model 2c: log(annual avg. inst. disch.) v. avg. of bio. data at a two year lag
Model 2d: annual avg. inst. disch. v. avg. of bio. data at a two year lag

Discharge Data

The annual average instantaneous discharge for each of the streams for each year (in liters per second), and the total of those averages were used in generation of the models (Table 1). The total of the annual average instantaneous discharges of all six streams rather than the average of the annual average instantaneous discharges of all six streams was input into each of the models. A total of the annual average instantaneous discharges of the six streams was used rather than an average because most of the years with "no data" actually had an annual average instantaneous discharge below the detection limit, so using an average would cause an overestimate in the data.

Flow Se	1991	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008
Aiken	ND	ND	28.07322	3.720747	16.62208	24.6424	25.5988	120.9387	15.76853	8.086514	454.53	4.03E-05	20.6037	45.7614	71.66195	37.93041	43.81401
Canada	239.6347	125.9702	51.18712	15.21844	36.9865	41.03453	31.95885	49.38814	34.85332	30.0612	279.2591	46.9644	35.79851	86.55839	91.77264	41.51424	94.32555
Delta	97.08636	54.46046	26.63434	0.907376	ND	ND	3.220027	10.79914	0.330611	0.23589	225.9808	11.05072	ND	31.48382	66.39338	61.11572	19.67286
Green	174.7678	95.33033	29.03328	12.99934	24.55042	31.86643	28.02566	53.35043	19.28957	ND	144.4614	30.1912	44.02162	79.46221	99.12136	67.21126	81.27698
L Seal	274.0508	196.2096	97.07271	11.42562	36.64347	24.37803	39.32259	56.05431	31.33219	11.25997	ND	ND	35.86324	110.6193	ND	ND	77.05641
Von G	81.0104	56.54867	27.75017	3.252204	6.221799	6.115293	0.9179	3.283816	ND	ND	135.6903	8.199299	10.27899	53.23771	17.33477	21.55335	11.60774
Total	866.55	528.5193	259.7508	47.52372	121.0243	128.0367	129.0438	293.8145	101.5742	49.64357	1239.922	96.40565	146.5661	407.1229	346.2841	229.325	327.7536

Table 1: Annual average instantaneous discharge data used in biological modeling. Units: liters/second

The discharge data were collected every fifteen minutes from stream gauges for the duration of the warm season each year of the program (with frequent data gaps from a few hours to a few weeks in length). There are gauges on nine of the thirteen streams that feed Lake Fryxell. Seven of these thirteen streams supply most of stream-borne fresh water to the lake (www.mcmlter.org). In this thesis, stream data from six of these seven streams were

used to run the correlations: Aiken Creek, Canada Stream, Delta Stream, Green Creek, Lost Seal Creek, and Von Guerard Creek (Table 1). A seventh main stream (McKnight Stream) was not used to generate the correlations because the gauge had fallen into disrepair. Each data point in a correlation (Appendix B) represents the annual average instantaneous discharge of each of the six gauged streams summed together for each year.

Due to the variability in stream discharge on daily, weekly, monthly, and yearly time scales, a statistical approach to answer the research question was used, rather than attempting a test of a physical model. To illustrate the variability in stream discharge, examples of two flow seasons (1998 – 1999 and 2001 – 2002) are displayed below. The 1998 – 1999 flow season for Canada Stream (Figure 2) is an example of a slightly above discharge year (Table 1). Note the timing of the beginning and ending of flow. The 2001 – 2002 flow season for Canada Stream, demonstrates the relative discharge of a very high flow year (Figure 3). The daily average instantaneous stream discharge into Lake Fryxell in this year was the highest of any flow season investigated. Contrast the discharge with that of Figure 2. Due to the extreme nature of the discharge event for this flow season, all models determined this flow season to be an outlier. The 2001 – 2002 year is the far right hand solid point (Figures B1 – B3 and B5 – B9 in Appendix B) on all of the models used to correlate the four different biological variables except for the alternate bacterial production model.

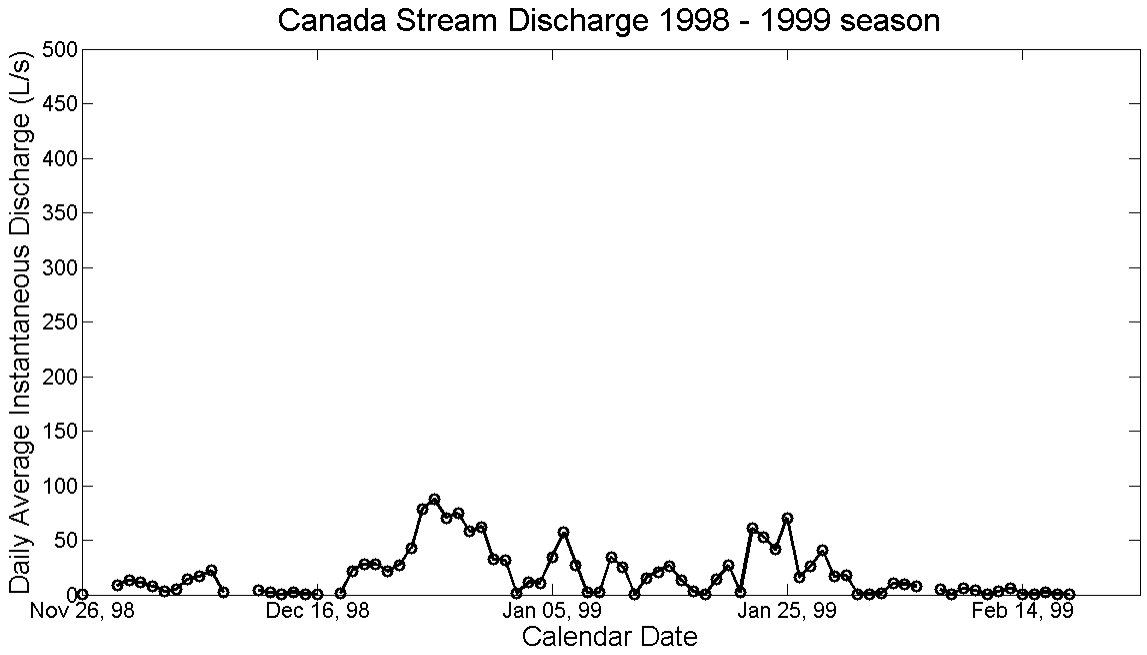

Figure 2: Canada Stream daily average instantaneous discharge for the 1998 to 1999 flow season.

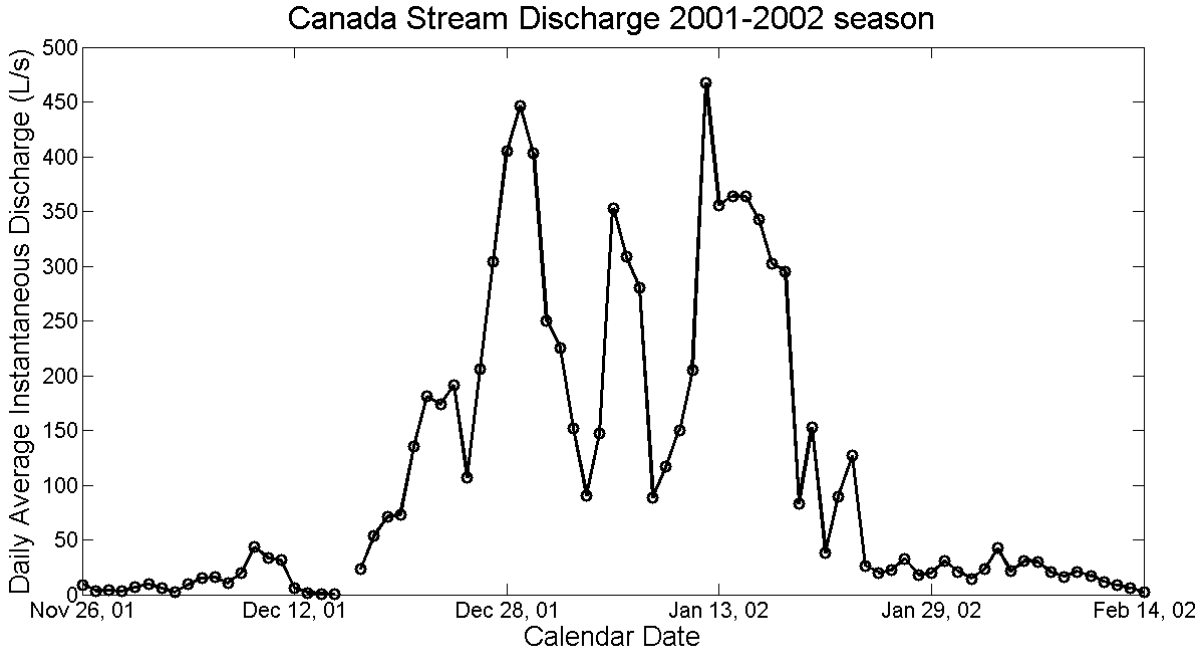

Figure 3: Canada Stream daily average instantaneous discharge for the 2001 to 2002 flow season.

Logarithmic Scale versus Linear Scale

The advantage of a logarithmic scale is that data extremes of high and low in the data are scaled into a tighter range. Details on very small and very large scales that would not otherwise be easily detectable often become apparent when employing a log scale. It is for this reason that log scales were used in creating the models. In Figure 4 a good example of how small but valid and significant trends are made apparent by the same logarithmic scaling process is displayed. The two plots in Figure 4 displaying the same data. Figure 4a shows the data with linear axes, while Figure 4b applies a log scale to both axes of the same data.

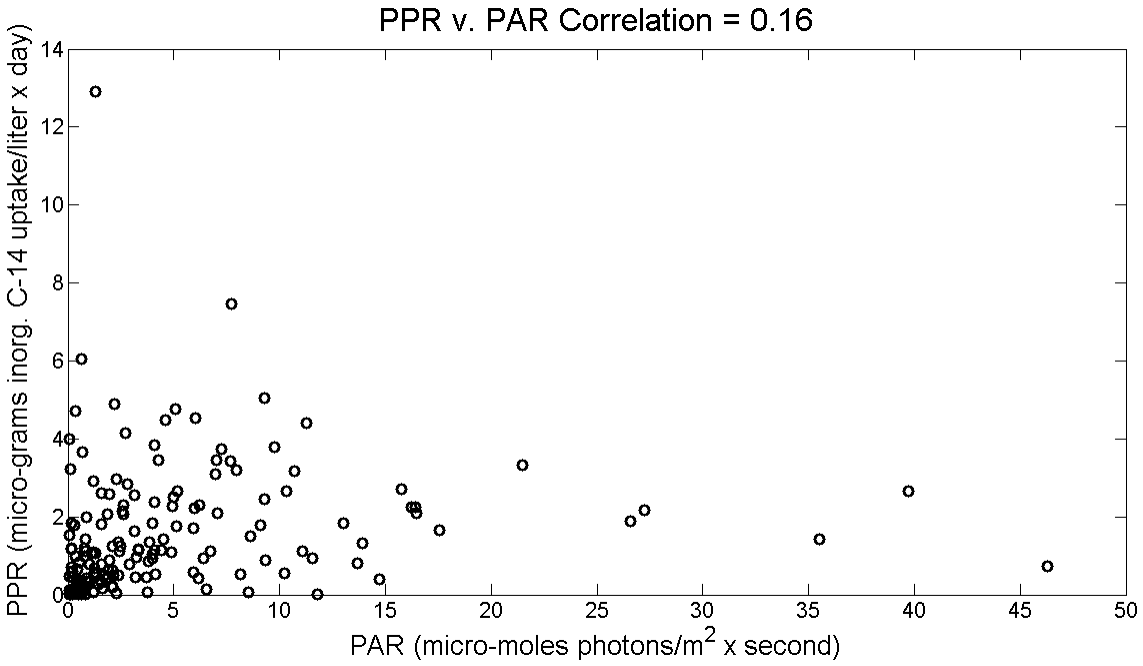

Figure 4a: Example of why using a logarithmic scale is useful, linear scale

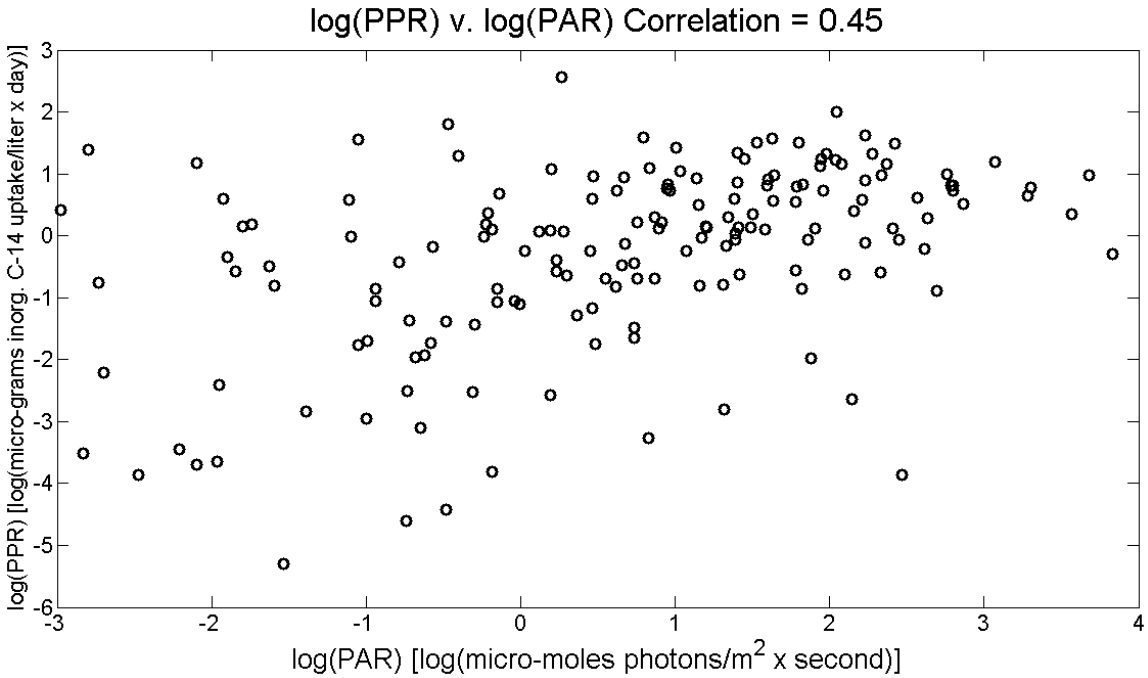

Figure 4a: Example of why using a logarithmic scale is useful, logarithmic scale

Lake Profiles

For the all of the Taylor Valley lakes, including Lake Fryxell, biological data were collected by MCM-LTER researchers three to four times per flow season. Zero depth is considered to be the point at the bottom of the lake ice cover. This poses some problems when comparing the data. The important reference is the chemocline: the boundary above the lake bottom that defines the beginning of the anoxic zone as depth increases. The height of the chemocline is nearly unchanged through time and is the most significant boundary in the water column because it divides the lake's different biological regimes. The thickness of the ice covering Lake Fryxell changes significantly over time (Figure 5). The changing thickness of the ice cover and change in volume of lake water over time means that the zero-lake-depth point moves up and down in space over time, which produces an artifact in the depth profile data in which the depth of the chemocline appears to change over time. In this thesis only data from eleven meters and above were assumed

to be in the oxygenated zone, and above the chemocline. Therefore, only data from eleven meters and above were incorporated into my analysis.

Lake profiles are presented in log form in this thesis. The linear scale is best for getting an idea of the true contrast in lake conditions with respect to time and depth, but usually most of the detail is lost. The log scale however is generally more practical for purposes of comparing subtle changes in lake conditions in time and space, and when comparing different lake conditions to one another.

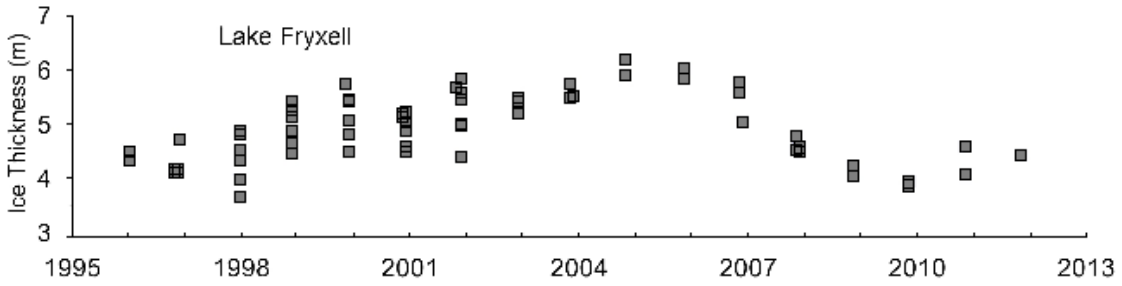

Figure 5: Thickness of the ice cover of Lake Fryxell at multiple locations over time. Figure courtesy of Peter Doran, data from MCM-LTER.

Averages

Averages were used to compute correlations between lake biological data and discharge data because there are hour to week long gaps in the discharge data and antire months or occasional random depths in the biological data. This occurs due to the seasonality of data collection and the infrequent occurrence of instrument malfunction, etc. Inspection of the lake profiles (depth versus time graphs) suggests the extent of this problem (Appendix A). Due to data gaps the discharge data are less than ideal since the stream discharge fluctuates wildly throughout the day and the flow season.

Outliers

Outliers were removed from the correlations displayed in the results section by applying the Cook's distance function in MATLAB. Cook's distance is a widely accepted mathematical method used to discriminate between outliers and non-outliers in a data set when applying a least squares linear regression (Dr. Radu Herbei, personal comm., 2012). The advantage of using a mathematical method to determine outliers is that it removes the bias of the researcher. Manually selecting points to remove can inadvertently lead to inaccurate results. There is more than one way to utilize cook's distance, for my algorithm, any point with a Cook's distance greater than four divided by the number of data points was deemed to be an outlier (Cook, 1977).

Four of the models were run a second time with a minor manual change. For bacterial production at a one year lag, the far right year was determined to be an outlier and removed prior to the computation of Cook's distance thus reducing the value of n (Figure B4 in Appendix B). This revealed that one or two points from each of the four re-run models had become outliers. It is this modified version that is shown in the results section, (Figure 11 left panel of the summary subsection), and all versions of this model are displayed in Figure B4, Appendix B.

Correlation Coefficient and Coefficient of Determination

The correlation coefficient is defined as the covariance of two different variables divided by their standard deviations multiplied together. It is expressed as a number between negative one and one. Covariance can be qualitatively described as how well two variables change together. If two variables increase together the covariance is a positive

number; if one variable increases as the other decreases then the covariance is a negative number. Standard deviation is a measure of how the data are distributed. A data set with a high standard deviation contains data that are spread far above and below the mean value. If the standard deviation is low, the data are clustered tightly around the mean value. Since in the process of generating a correlation coefficient the standard deviations of the two data sets are multiplied together and placed in the denominator, large standard deviations significantly reduce the value of the correlation coefficient.

A correlation coefficient of one would represent a perfectly straight line of points that can be described as points lying along a line with a positive slope. A correlation coefficient of negative one would represent a perfect line of points that can be described as lying on a line that has a negative slope. The slope of the line is irrelevant when determining the correlation coefficient. Only how well the line describes the location and trend of the points has any bearing on the determination of the correlation coefficient. A correlation of zero would mean that the data points display no linear trend at all.

Once the correlation coefficient is established, the next step is to generate the coefficient of determination, otherwise known as the R^2 value. The coefficient of determination is simply the correlation coefficient squared. This number (expressed as a percent) is used to predict outcomes of the dependent variable using only the independent variable. If a comparison of two variables yields a coefficient of determination of 55% it means that 55% of the changes in the dependent variable can be explained by changes in the independent variable.

Biological Data Used for Modeling

The biological data input into the models employed in this thesis included primary production (PPR), bacterial production (BP), chlorophyll-a concentration (Chyl-a), bacterial enumeration (BE). Each cell represents an average of the biological variable in the top eleven meters of the water column. The stream waters enter the lake directly beneath the ice due to their very low density resulting from high initial temperature and low salinity (W. Berry Lyons, personal comm., 2011). Because stream waters remain at the very top of the water column, only the top eleven meters of the water column (above the chemocline) were considered when correlating these biological variables with annual average instantaneous stream discharge. A very brief description of the collection and treatment of samples for each of the four types of biological variables follows.

Flow Season:	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007
PPR	10.264	2.972	1.582	0.507	1.386	2.798	2.302	2.266	4.510	1.433	1.186	1.851	1.983	ND
BP	0.132	0.184	0.075	0.110	0.124	0.186	0.254	0.103	0.103	0.019	0.021	0.033	0.009	ND
Chyl-a	13.752	14.547	6.367	8.814	22.660	12.943	12.534	11.370	9.607	6.260	6.409	6.828	7.219	17.076
BE	ND	ND	ND	ND	ND	3584182	ND	1924909	1807900	948600	1467250	1890944	4237778	5234222

Table 2: Biological data used in modeling (www.mcmlter.org).

Primary Production (PPR)

PPR is measured as micrograms of inorganic C-14 uptake per liter day [µg inorg. C-14 uptake/liter*day]. PPR is a measure of planktonic autotrophic activity. The process of collecting samples for generation of PPR data involves multiple steps. First, starting at the lake ice surface, two water samples are collected at each point along a one meter depth interval at the same location. These samples are collected zero to three times a year at roughly one month intervals. Second, the in-solution isotope carbon-14 is added to all the

bottles. Third, both bottles are returned to their original depth and left suspended on a line for twenty four hours. One bottle at each depth is a control and is opaque; the other is transparent so that light can penetrate. Fourth, the bottles are removed from the lake, the phytoplankton components are filtered out and isolated, and carbon-14 uptake is measured in a laboratory. Fifth, the carbon-14 uptake from each control bottle is subtracted from the carbon-14 uptake measured in each of the transparent bottles from the same depth. Further details on the collection and treatment of PPR samples are available at www.mcmlter.org.

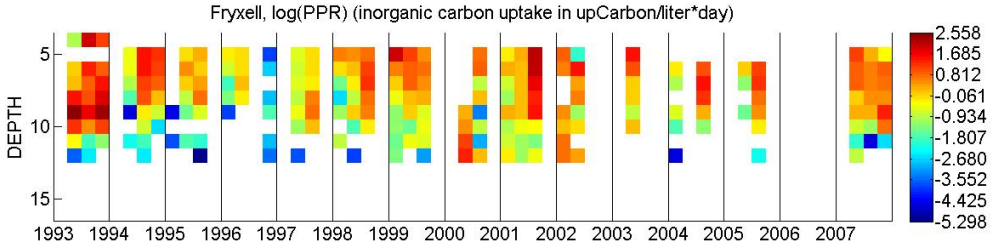

Figure 6: Graphic representation of the logarithmic scaled original PPR data (www.mcmlter.org). Important note: "No data," "PPR below the detection limit," and "negative PPR" are represented by white spaces.

Bacterial Production (BP)

BP is measured as the thymidine uptake rate using tritiated thymidine [nMTDR/day]. BP is a measure of planktonic bacterial heterotrophic activity. Properly explaining the method of collection and analysis of these samples would require several pages and branch into several other disciplines that are not the focus of this study. The details of the methodology behind collection of these samples and generation of the data can be found at the MCM-LTER website: www.mcmlter.org.

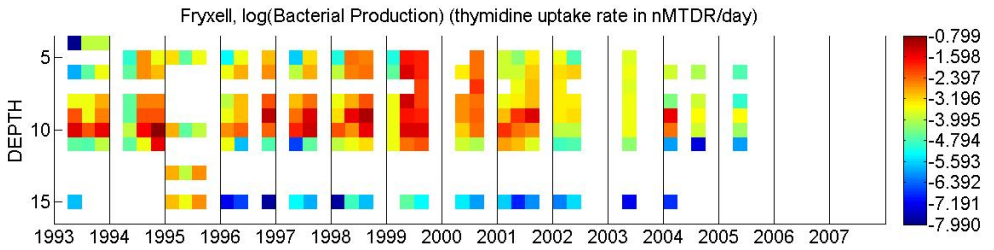

Figure 7: Graphic representation of the logarithmic scaled original BP data (www.mcmlter.org). Important note: "No data," "BP below the detection limit," and "negative BP" are represented by white spaces.

Chlorophyll-a Concentration (Chyl-a)

Chyl-a is measured as chlorophyll-a per liter [µg Chyl-a/liter]. Chyl-a concentration is a measure of planktonic autotrophic biomass. It is important to note that some portion of the lake's plankton species are both autotrophic and heterotrophic, meaning they are able to photosynthesize and consume organic matter for energy. Chyl-a concentration is measured by filtering water samples through a glass fiber filter that filters out phytoplankton. The chlorophyll-a from the phytoplankton is then isolated using 90% acetone on the filter. The isolated chlorophyll-a is then analyzed using a fluorescence technique. Further details are available on the MCM-LTER website: www.mcmlter.org.

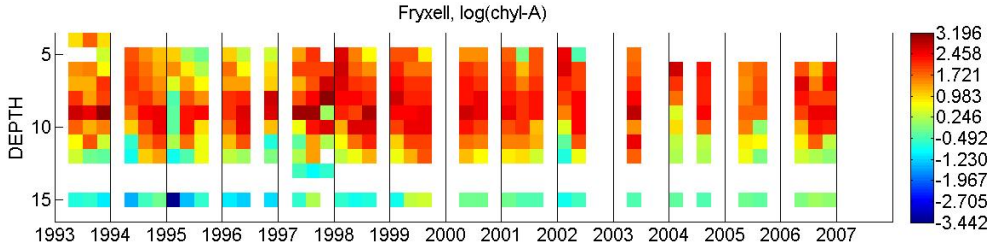

Figure 8: Graphic representation of the logarithmic scaled original Chyl-a data (www.mcmlter.org). Important note: both "no data" and "Chyl-a below the detection limit" are represented by white spaces.

Bacterial Enumeration (BE)

BE is a direct count of the number of cells in a given milliliter of sampled water [cells/ml]. BE is a proxy of bacterial biomass. Many different individual species have been identified and counted by the MCM-LTER, but in this thesis only the total count of all the bacteria present was considered in the models. It is measured using a fluorescence technique involving SYBR® Gold. Further details regarding the collection and analysis of BE samples are available at the MCM-LTER website: www.mcmlter.org.

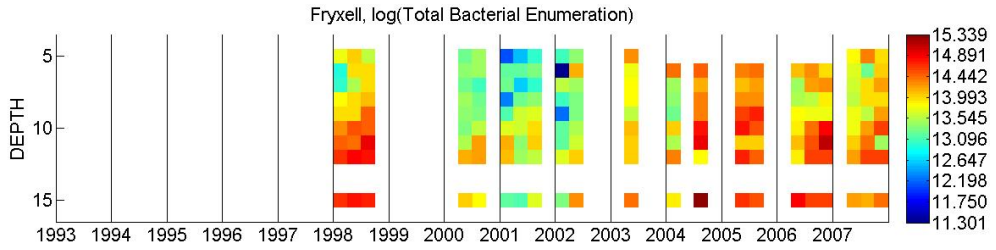

Figure 9: Graphic representation of the logarithmic scaled original BE data (www.mcmlter.org). Important note: both "no data" and "BE below the detection limit" are represented by white spaces.

Results

Summary

The model that was most successful at predicting biological activity was the log of annual average instantaneous discharge versus a linear scale of biological activity at a two year lag between discharge data and biological activity data (Figure 10, model type 2c). Each point represents one year. The dashed trend line represents a liner regression based on all data points, and the solid trend is based just on the hollow points (solid points are outliers). Eight models were generated for each of the four biological parameters (Appendix B).

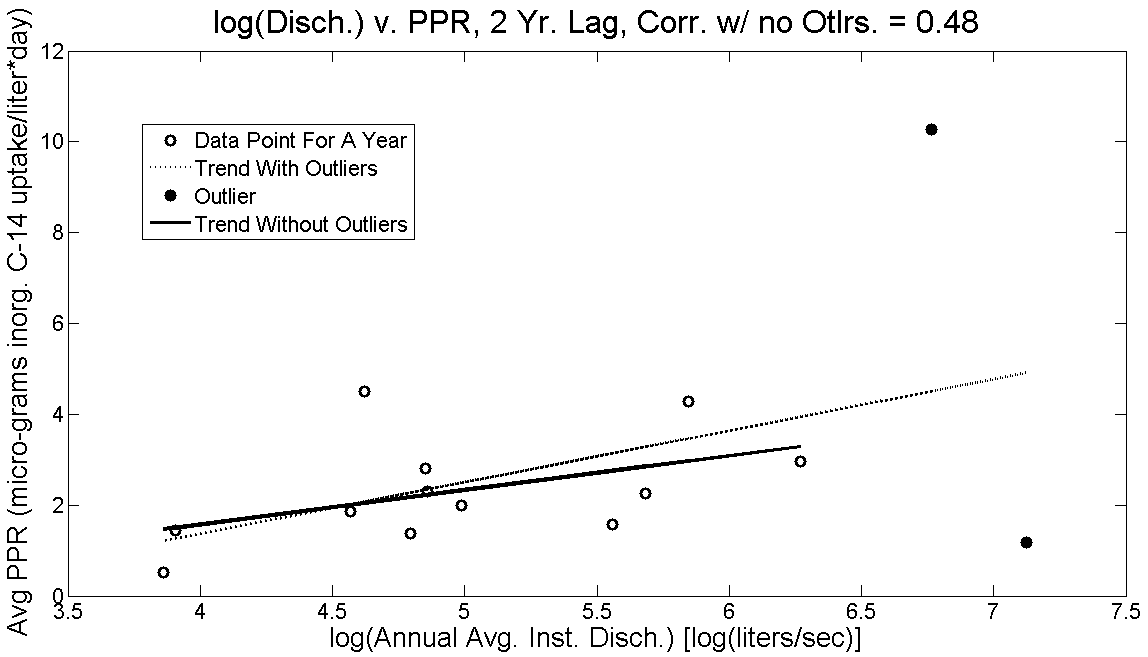

Figure 10a: Results of model 2c applied to PPR.

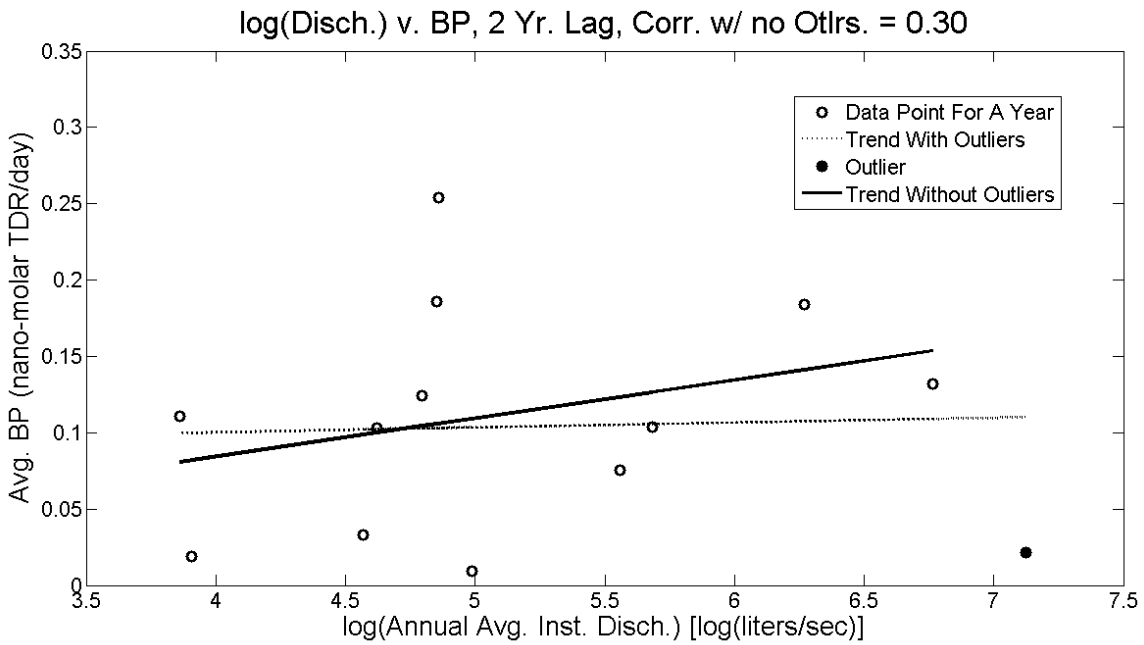

Figure 10b: Results of model 2c applied to BP.

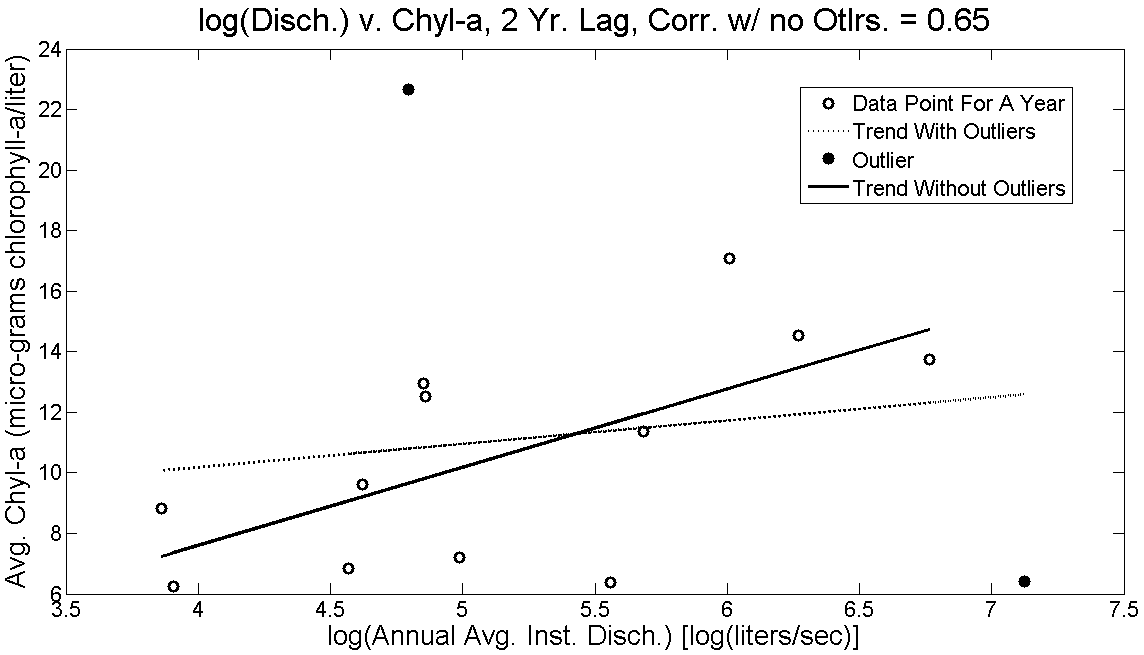

Figure 10c: Results of model 2c applied to Chyl-a.

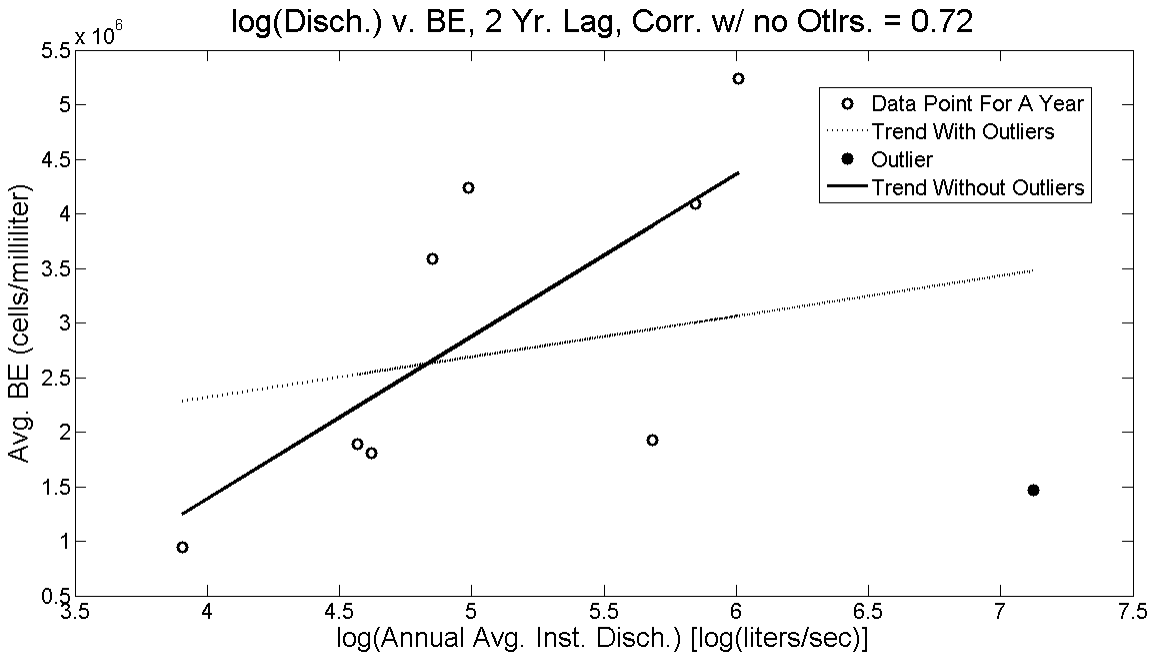

Figure 10d: Results of model 2c applied to BE.

There were two cases where the most successful model type did not yield the best correlation. Both of these cases are model 1c (Figure 11), they are the same as the most successful model with the single difference that these employ a one year lag, whereas model 2c employs a two year lag. The dashed trend line represents a liner regression based on all data points, the solid trend is based only on the hollow points (solid points are outliers). Note: the correlation for another model of BE at a one year lag was 0.01 higher, (Figure B8 in Appendix B) and the highest flow year outlier was removed manually from the BP model shown here before applying Cooks distance (Figures B3 and B4 in Appendix B).

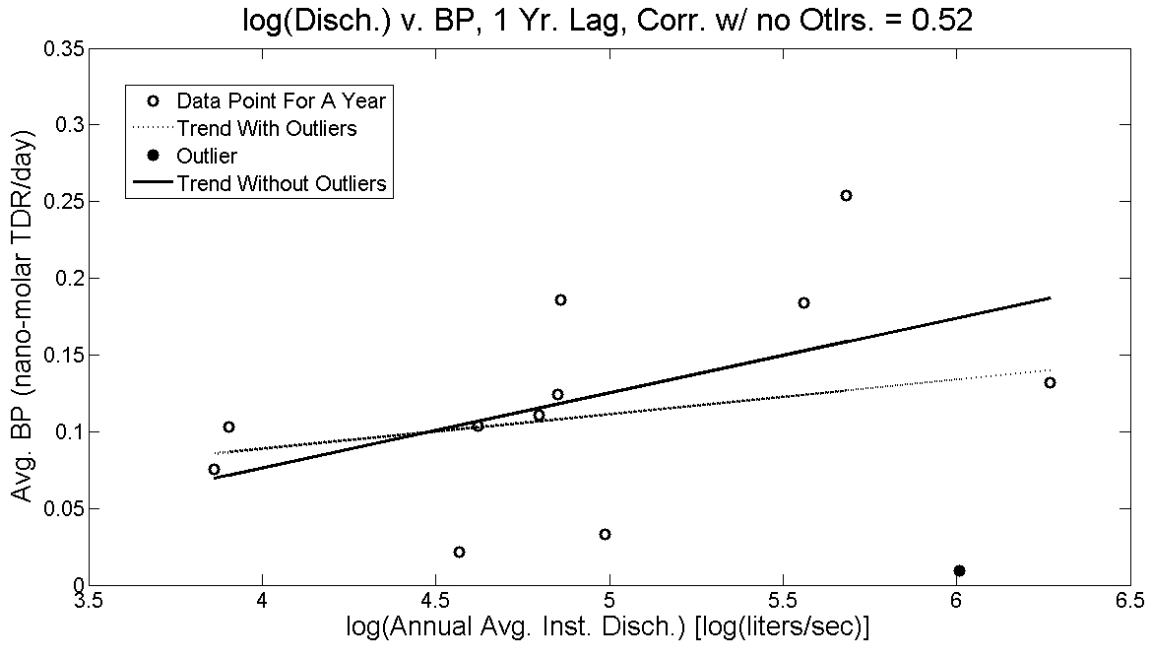

Figure 11a: A BP result better than model 2c BP; model 1c BP.

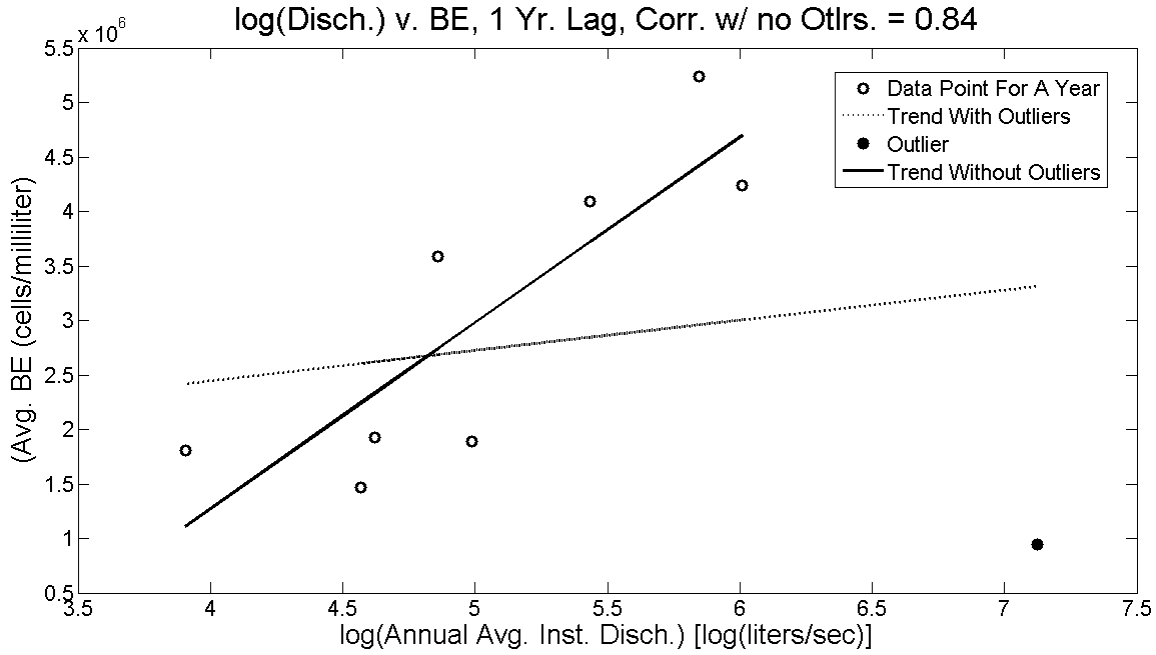

Figure 11b: A BE result better than model 2c BE; model 1c BE.

Primary Production

The strongest correlation was in the most successful model type: model 2c – log(annual average instantaneous discharge) v linear(biological variable) at a two year lag – with a correlation coefficient of 0.48 and a coefficient of determination of 23%. Of the one year lag models the best correlation coefficient came from model 1a – the log-log model – and was 0.41 with a coefficient of determination of 17% (Figures B1 and B2 in Appendix B).

Bacterial Production

Twelve rather than eight correlations were produced for bacterial production, see the "outliers" subsection of the methods section for details. The strongest correlation here was in model 1c – log-linear at a one year lag – with a correlation coefficient of 0.52 and a coefficient of determination of 27%. Of the two year lag models the best correlation coefficient came from model 2a – the log-log model – with a correlation of 0.34 and a coefficient of determination of 12%. The most successful model type, model 2c, did not do as good of a job of predicting bacterial production. It produced a coefficient of determination of 0.30 and a coefficient of determination of only 9% (Figures B3, B4, and B5 in Appendix B).

Chlorophyll-a Concentration

The strongest correlation of all model types applied to chlorophyll-a was also the most successful model type: model 2c – log(annual average instantaneous discharge) v linear(biological variable) at a two year lag – with a correlation coefficient of 0.65 and a

coefficient of determination of 42%. Of the one year lag models, the best correlation coefficient came from model 1a – the log-log model – and was 0.38 with a coefficient of determination of 15% (Figures B6 and B7 in Appendix B).

Bacterial Enumeration

The strongest correlation found for bacterial enumeration was the best of all of the correlations found. All four models displaying a one year lag (models 1a through 1d) all produced correlation coefficients between 0.820 and 0.845, and coefficients of determination between 68% and 71%. In the two-year-lag models, model 2c produced the best coefficient of determination at 51% (Figure B8 and B9 in Appendix B).

Discussion

Bacterial Processes versus Photosynthetic Processes

Bacterial production and bacterial enumeration showed a strong correlation with stream water input at a one year lag while primary production and chlorophyll-a concentration showed a strong correlation at a two year lag with stream water input. The difference in response time between bacterial processes and photosynthetic processes may be explained by the difference in nutrients used by each. I assume that any increase in discharge will increase the addition of nutrients into the lake: carbon, nitrogen, and phosphorus (McKnight et al., 1999). Bacteria respond to the input of particulate organic matter in the incoming stream water. Particulate organic matter serves two main purposes for bacteria: first, it is a primary food source for bacteria, and second, most planktonic bacteria spend most of their existence adhered to particles suspended in the water. Phytoplankton on the other hand are dependent on dissolved inorganic carbon, nitrogen, and phosphorus (Moss 1998).

The difference in how these two nutrient species disperse throughout the water column may account for the difference in the lag of the models that best describe bacterial activity (one year lag) and photosynthetic activity (two year lag). Fresh stream water first settles directly beneath the ice and begins to cool down. As it sits, particulate matter settles out of the freshly input stream water and falls to depths in the water column. This interaction between bacteria and descending particulate matter in the water column may be primarily responsible for the correlation observed between stream flow and bacterial activity.

The transport of nitrogen, phosphorus, and dissolved inorganic carbon on the other hand is primarily driven by diffusion or minimal small scale density driven mixing as the newly input stream water cools and freezes (W. Berry Lyons, personal comm., 2012). Diffusion of these nutrients down through the water column under these conditions is suspected to take longer than the decent of particulate matter. Diffusion in Lake Fryxell is slow enough that there is a perpetual salinity gradient between roughly 6700 milligrams of salt per liter and 200 milligrams of salt per liter across only fifteen meters of water depth (Figure A3 in Appendix A). That is about twice the salinity of the ocean near the bottom of the lake, to fresh water at the top of the water column. Another possibility is when the stream water at the surface of the lake begins to cool and freeze onto the lake's water-ice surface, increasing its salinity through the process of ion exclusion from ice as the water freezes. The density of the water then increases to a point where it begins to mix slightly into the upper waters of the lake. This process may take more than one winter to occur, hence the two year lag (W. Berry Lyons, personal comm., 2012).

The Success of the "C" model

Four models (dubbed models a through d) were applied to each of the two possible lags, (one year and two year), to produce a total of eight models to explain variations in each of the four measured biological variables: PPR, BP, Chyl-a, and BE. Whether it was in a one year lag model or a two year lag model, the best correlation was always given by a "c" model. C models all use a linear scale for the biological data, but a log scale for the discharge data. This implies that past a certain annual average instantaneous discharge value, additional stream flow has less and less of an effect on lake ecology. This is known as

the point of diminishing return. I explain this finding by hypothesizing that the nutrients provided by the streams are no longer the limiting nutrient for the lake's planktonic organisms, or that some other process related to stream flow limits plankton growth. A few of these other possible processes include water temperature, O_2 availability, predation, and viral lysing.

Correlation versus Causation

In this thesis fluctuations in biological activity were compared to changes in stream flow. It is very important to point out that stream flow was not the only physical parameter changing with time. Variations in stream flow are a reflection of climatic conditions, namely air temperature, cloud cover, and wind strength. These same meteorological conditions also have an effect on the thickness of the ice cover, the width of the melted zone around the lake edge or "moat" (which promotes gas exchange), the amount of light available for photosynthesis, and mixing around the lake edge and build up wind-blown dust on the lake ice surface. In addition, only a few in-lake processes were considered in drawing conclusions about the correlation between stream flow and changes in biological parameters. All these processes could be influenced by the same climatic conditions that drive stream flow, and could all have an impact on the measured biological parameters. Therefore more work is needed to verify the findings presented in this paper by exploring other correlations between biological parameters and climate induced physical conditions.

Conclusions

The models which showed a direct relationship between biological parameters and the log of annual average instantaneous stream discharge were most successful. The analysis presented herein suggests that stream water input into Lake Fryxell has a more profound effect upon the lake's planktonic biomass than on the lake's planktonic productivity. Bacterial production and bacterial enumeration showed the best correlation to annual average instantaneous stream discharge from the year before. Primary production and chlorophyll-a concentration showed the best correlation to the annual average instantaneous stream discharge of two years prior. I hypothesize that the difference between these two observations is due to the difference in nutritional needs of bacteria and plants.

Recommendations for Future Work

In the McMurdo Dry Valley lakes, there are many factors that influence biological parameters, some of which are determined by climatic conditions. Further work is needed to constrain the other variables that affect bacterial production, bacterial concentrations, primary production, and plant biomass. Changes in stream flow also may show strong correlations to other climatically controlled variables that simultaneously affect biological parameters. Climatic conditions such as changes in air temperature, cloud cover, and wind affect not only stream flow, but also the thickness of the ice cover, the width of the "moat" or melted zone around the lake edge (which promotes gas exchange), the amount of light available for photosynthesis, mixing, and the accumulation of dust on the lake ice surface. Climate-driven shifts in dominant plankton species, and a host of other lake processes were not considered in this thesis. Statistical comparisons of biological parameters to average incoming solar radiation and average air temperature would enhance the understanding of what controls biological production and biomass within the lake. Furthermore, I also recommend making statistical comparisons between stream flow and incoming solar radiation as well as between stream flow and average air temperature to investigate what climatic conditions promote stream flow the most.

References

Cook, R.D., 1977, Detection of Influential Observation in Linear Regression: Technometrics, v. 19, p. 15-18.

Fountain, A.G., Lyons, W.B., Burkins, M.B., Dana, G.L., Doran, P.T., Lewis, K.J., McKnight, D.M., Moorhead, D.L., Parsons, A.N., Priscu, J.C., Wall, D.H., Wharton, R.A., and Virginia, R.A., 1999, Physical Controls on the Taylor Valley Ecosystem, Antarctica: Bioscience, v. 49, p. 961-971.

Fritsen, C. H., E. E. Adams, C. P. McKay, and J. C. Priscu., 1988, Permanent Ice Covers of the McMurdo Dry Valleys Lakes, Antarctica, Liquid Water Contents: Ecosystem Dynamics in a Polar Desert, The McMurdo Dry Valleys, Antarctica, J. C. Priscu, Editor, 269-280.

Herbei, R., Lyons, W. Berry, Laybourn-Parry, J., Gardner, C., Priscu, J.C., and McKnight, D.M., 2010, Physiochemical properties influencing biomass abundance and primary production in Lake Hoare, Antarctica: Ecological Modelling, v. 221, p. 1184-1193.

Lizotte, M.P., and Priscu, J.C., 1992, Photosynthesis-Irradiance Relationships in Phytoplankton from the Physically Stable Water Column of a Perennially Ice-Covered Lake (Lake Bonney, Antarctica). Journal of Phycology, v. 28.

Lyons, W Berry, K A Welch, , and P Sharma., 1998 Chlorine-36 in the Waters of the Mcmurdo Dry Valley Lakes, Southern Victoria Land, Antarctica: Revisited. Geochimica Et Cosmochimica Acta, 62.2: 185.

McMurdo Dry Valleys Long Term Ecological Research (MCM-LTER), http://www.mcmlter.org/, 1993, National Science Foundation Office of Polar Programs, last updated Oct. 15, 2012

Moss, B., 1998, Ecology of fresh waters : man and medium, past to future: Oxford [Eng.]; Malden, MA, Blackwell Science.

Priscu, J.C., 1995, Phytoplankton nutrient deficiency in lakes of the McMurdo Dry Valleys, Antarctica: Freshwater Biology., v. 34, p. 215.

Priscu, J.C., Wolf, C.F., Takacs, C.D., Fritsen, C.H., Laybourn-Parry, J., Roberts, E.C., Sattler, B., and Lyons, B., 1999, Carbon Transformations in a Perennially Ice-Covered Antarctic Lake: Bioscience, v. 49, p. 997-1008.

Appendix A: Physical and Chemical Lake Profiles

Physical Conditions

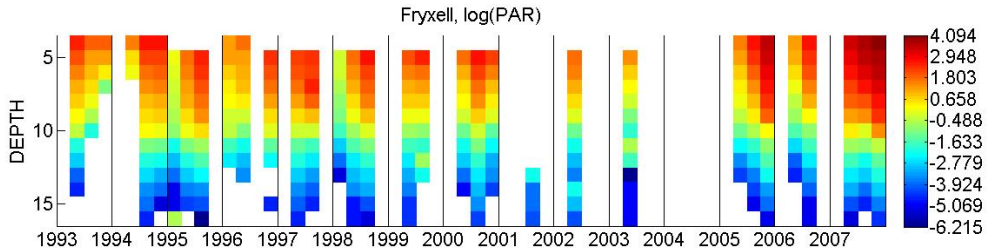

Figure A1: Graphic representation of the logarithmic scaled original photosynthetically active radiation data (www.mcmlter.org). Note: both "no data" and "PAR below the detection limit" are represented by white spaces. PAR unit: micro-moles of photons per square meter per second.

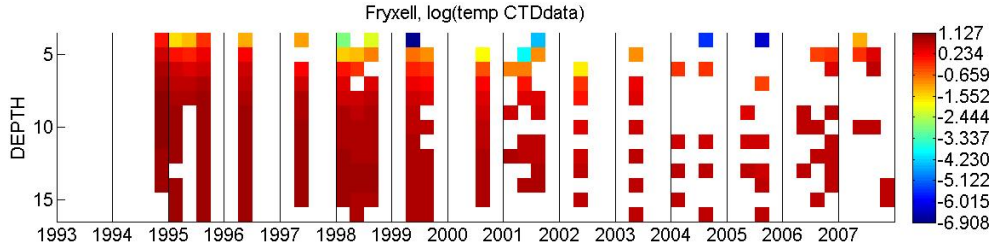

Figure A2: Graphic representation of the logarithmic scaled original temperature data (www.mcmlter.org). Note: both "no data" and a temperature of zero are represented by white spaces. Temperature unit: degrees Celsius.

Ion Chemistry

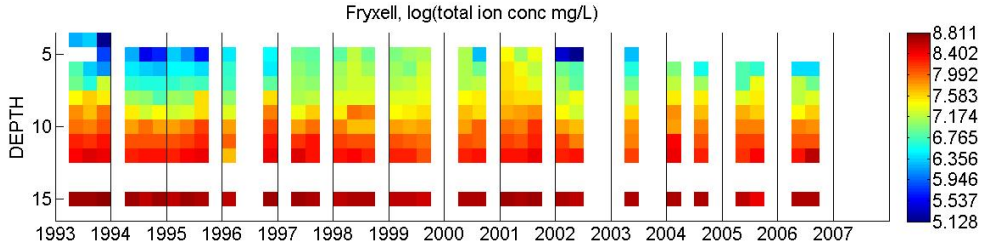

Figure A3: Graphic representation of the logarithmic scaled original salinity data (www.mcmlter.org). Note: white spaces represent "no data." Ion concentration unit: milligrams per liter.

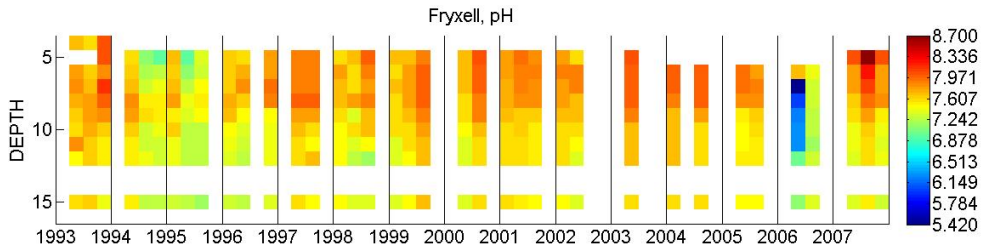

Figure A4: Graphic representation of the original pH data (www.mcmlter.org). Note: white spaces represent "no data"

Ammonia (NH_4)

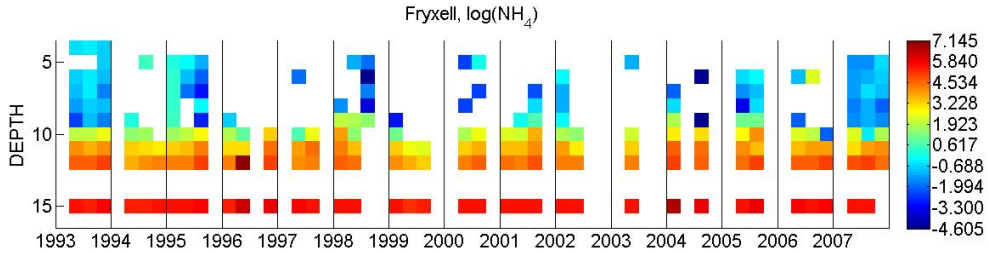

Figure A5: Graphic representation of the logarithmic scaled original ammonia concentration data (www.mcmlter.org). Note: both "no data" and "ammonia below the detection limit" are represented by white spaces. Ammonia concentration unit: micro-molar.

Soluble Reactive Phosphorus

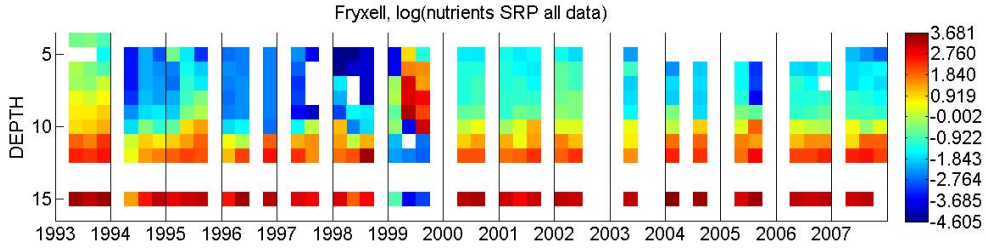

Figure A6: Graphic representation of the logarithmic scaled original SRP concentration data (www.mcmlter.org). Note: both "no data" and "SRP below the detection limit" are represented by white spaces. SRP concentration unit: micro-molar.

Carbon

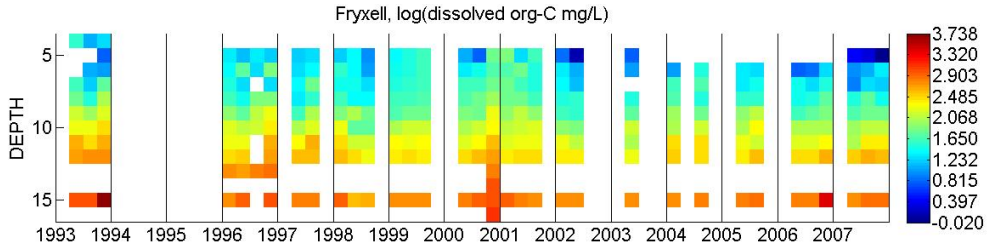

Figure A7: Graphic representation of the logarithmic scaled original dissolved organic carbon concentration data (www.mcmlter.org). Note: both "no data" and "DOC below the detection limit" are represented by white spaces. DOC concentration unit: milligrams per liter.

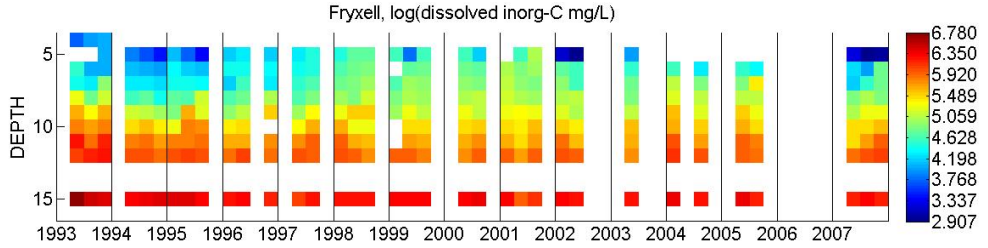

Figure A8: Graphic representation of the logarithmic scaled original dissolved inorganic carbon concentration data (www.mcmlter.org). Note: both "no data" and "DIC below the detection limit" are represented by white spaces. DIC concentration unit: milligrams per liter. Dissolved inorganic carbon generally consists of CO_2 and CO_3.

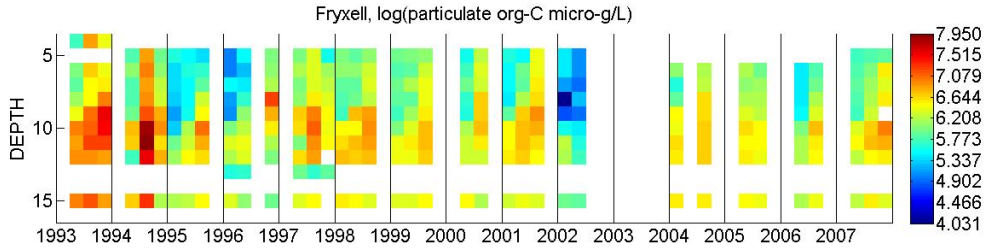

Figure A9: Graphic representation of the logarithmic scaled original particulate organic carbon data (www.mcmlter.org). Note: both "no data" and "particulate organic carbon below the detection limit" are represented by white spaces. Particulate organic carbon unit: micrograms per liter.

Nitrogen

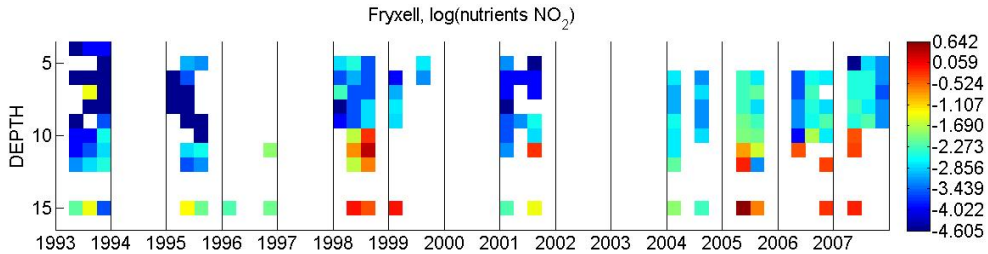

Figure A10: Graphic representation of the logarithmic scaled original NO_2 concentration data

(www.mcmlter.org). Note: both “no data” and “NO_2 below the detection limit” are represented by white spaces. NO_2 concentration unit: micro-molar.

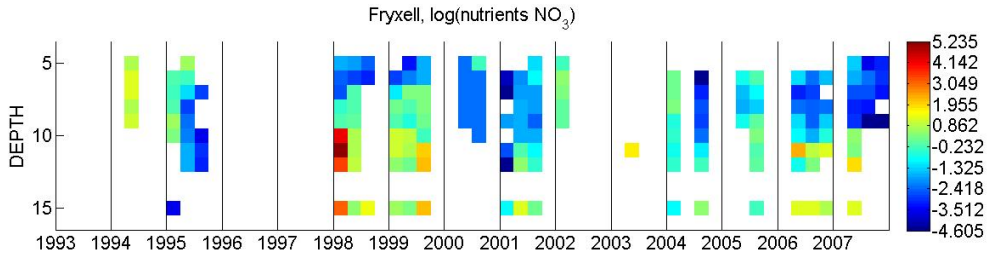

Figure A11: Graphic representation of the logarithmic scaled original NO_3 concentration data (www.mcmlter.org). Note: both “no data” and “NO_3 below the detection limit” are represented by white spaces. NO_3 concentration unit: micro-molar.

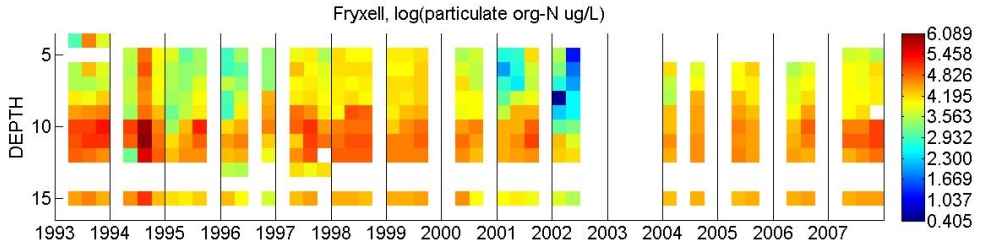

Figure A12: Graphic representation of the logarithmic scaled original particulate organic nitrogen concentration data (www.mcmlter.org). Note: both “no data” and “organic nitrogen below the detection limit” are represented by white spaces. Particulate organic nitrogen data unit: micrograms per liter.

Appendix B: Complete Results;

Models of Discharge Data versus Biological Data

The following figures are the complete results of all of the models tested in the effort of correlating biological data with stream discharge data. The "summary" subsection of the methods section details how each plot is generated and the reasoning behind it. In each of the following plots, a data point represents one year. The dashed trend line represents a liner regression based on all data points, and the solid trend is based off of only the hollow data points (solid points are outliers).

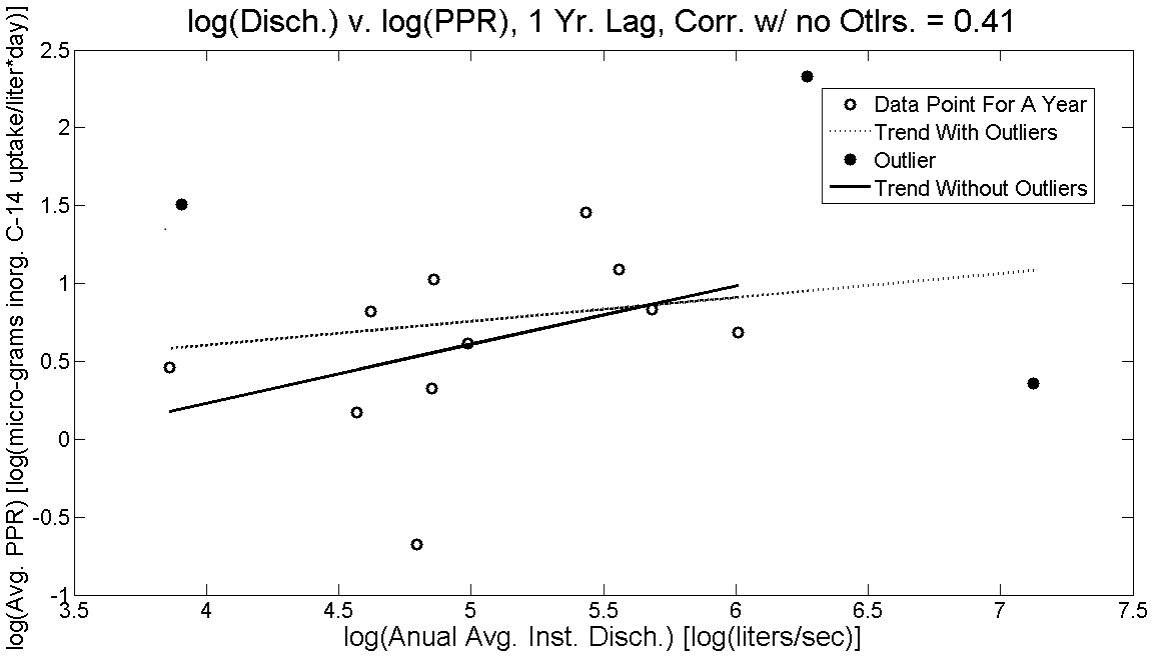

Figure B1a: log(annual average instantaneous discharge) v. log(primary production), 1 year lag.

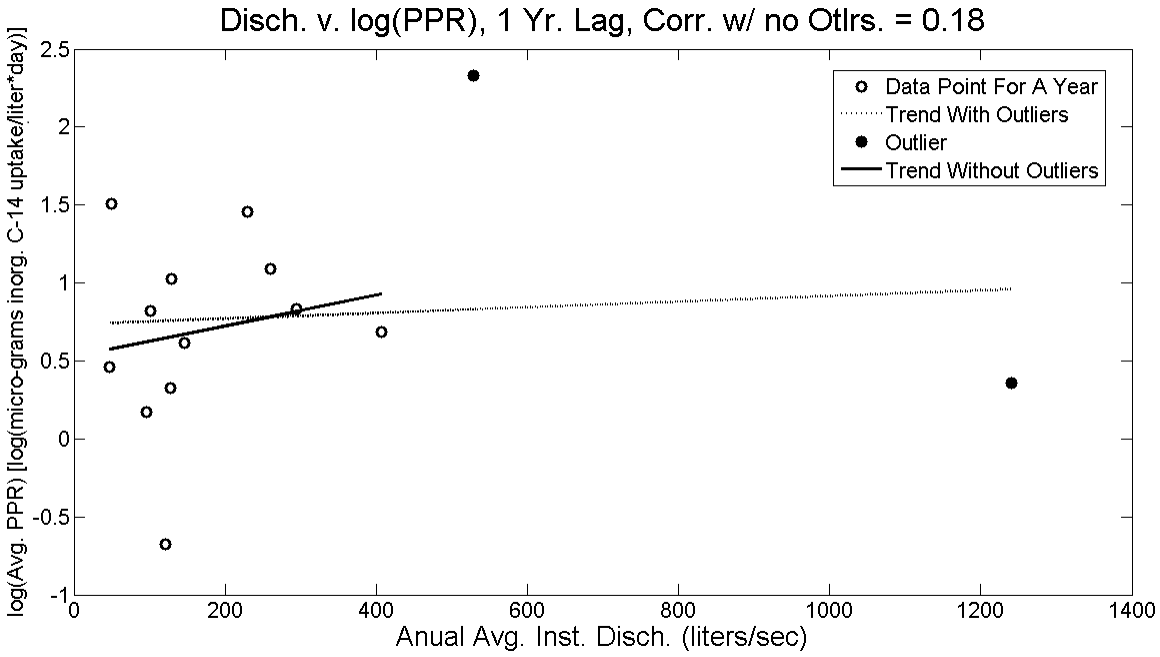

Figure B1b: annual average instantaneous discharge v. log(primary production), 1 year lag

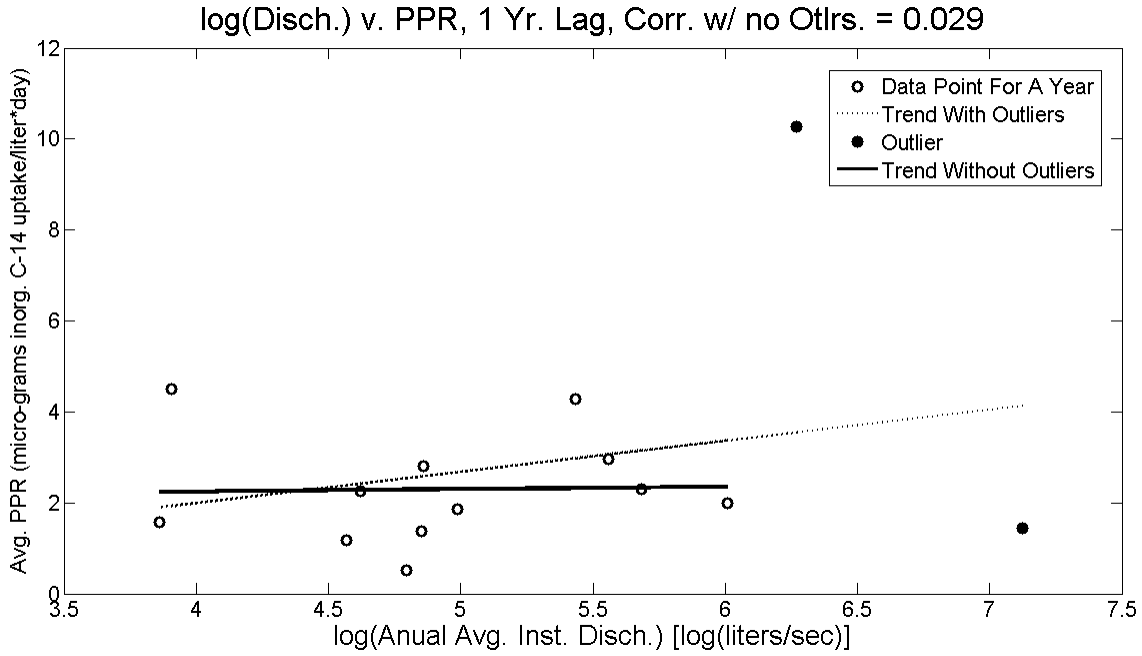

Figure B1c: log(annual average instantaneous discharge) v. primary production, 1 year lag.

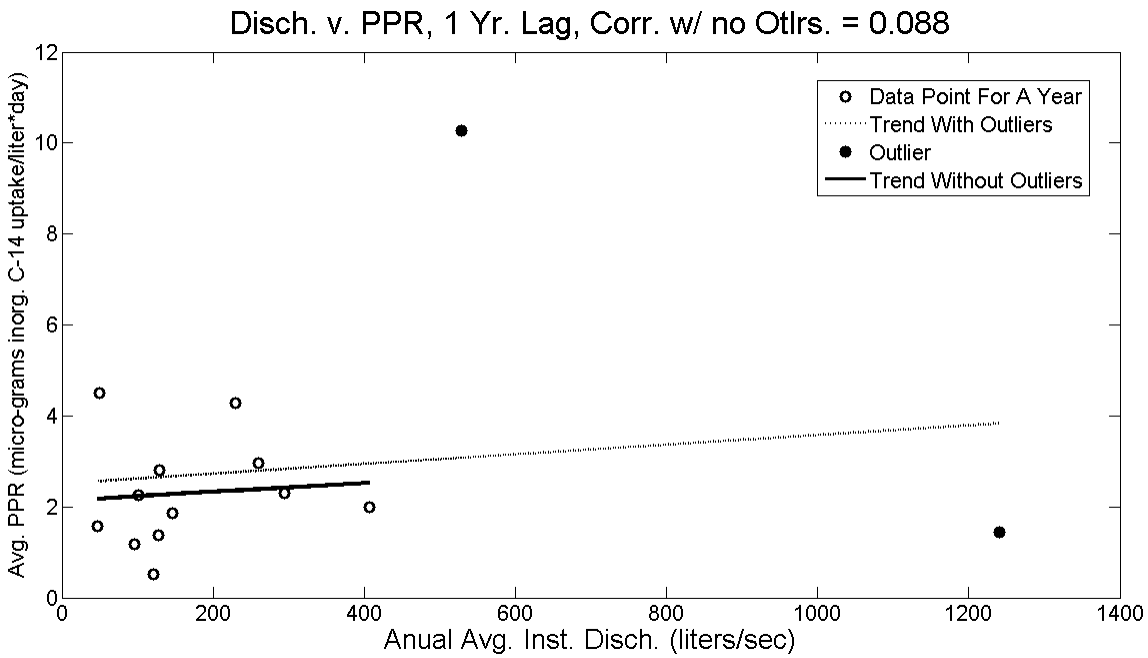

Figure B1d: annual average instantaneous discharge v. primary production, 1 year lag.

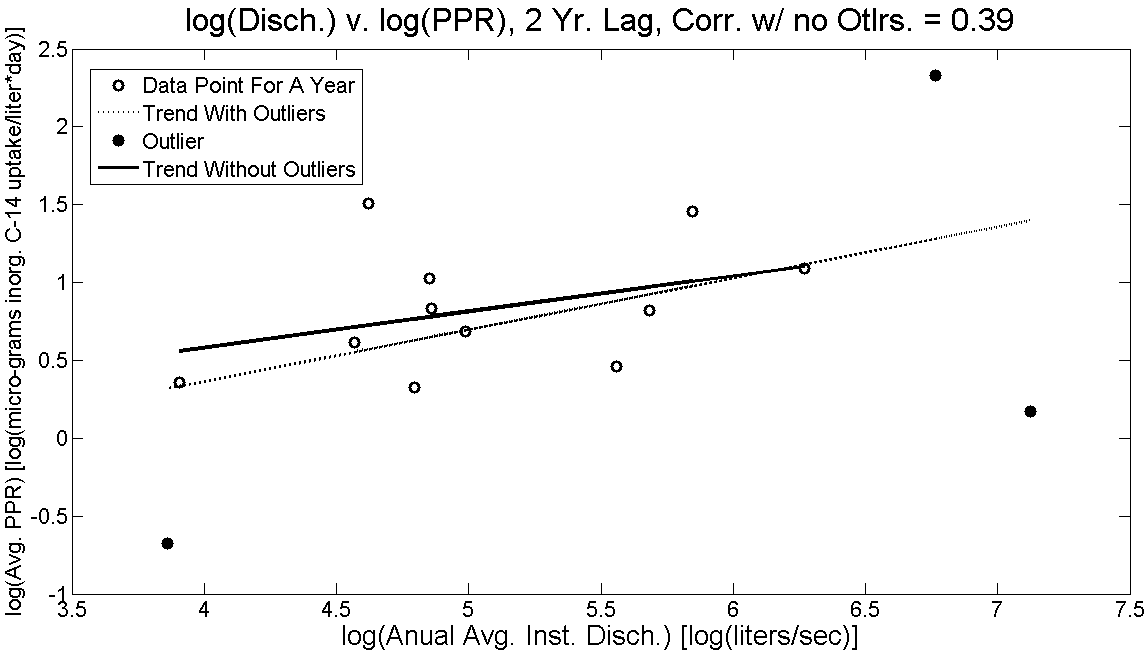

Figure B2a: log(annual average instantaneous discharge) v. log(primary production), 2 year lag.

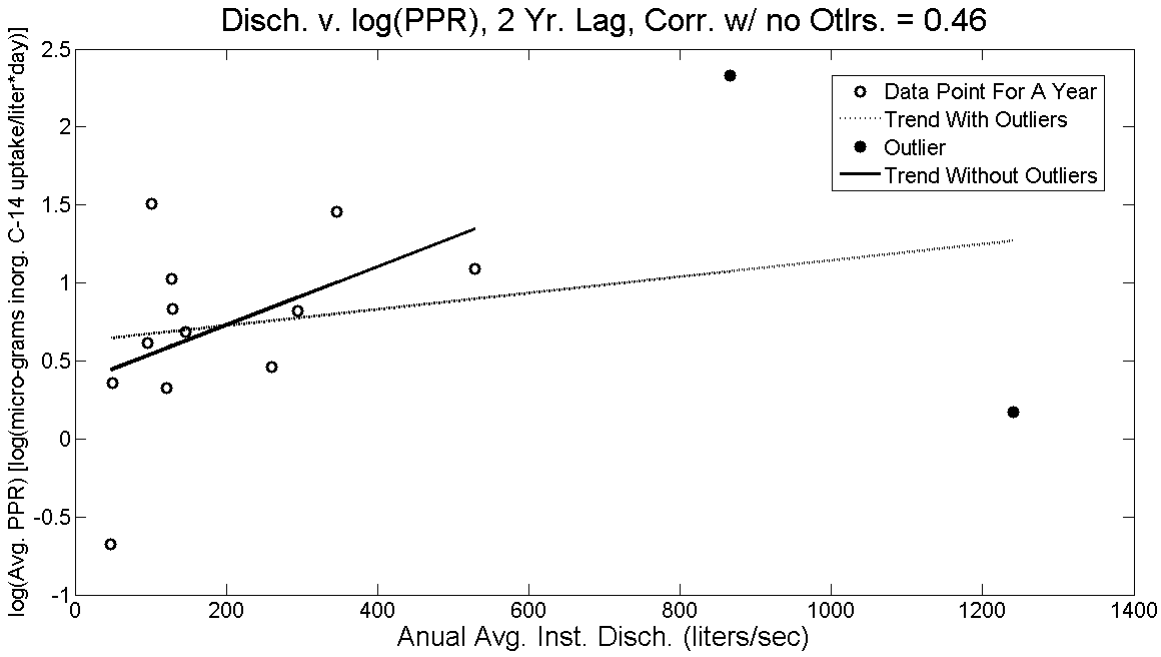

Figure B2b: annual average instantaneous discharge v. log(primary production), 2 year lag.

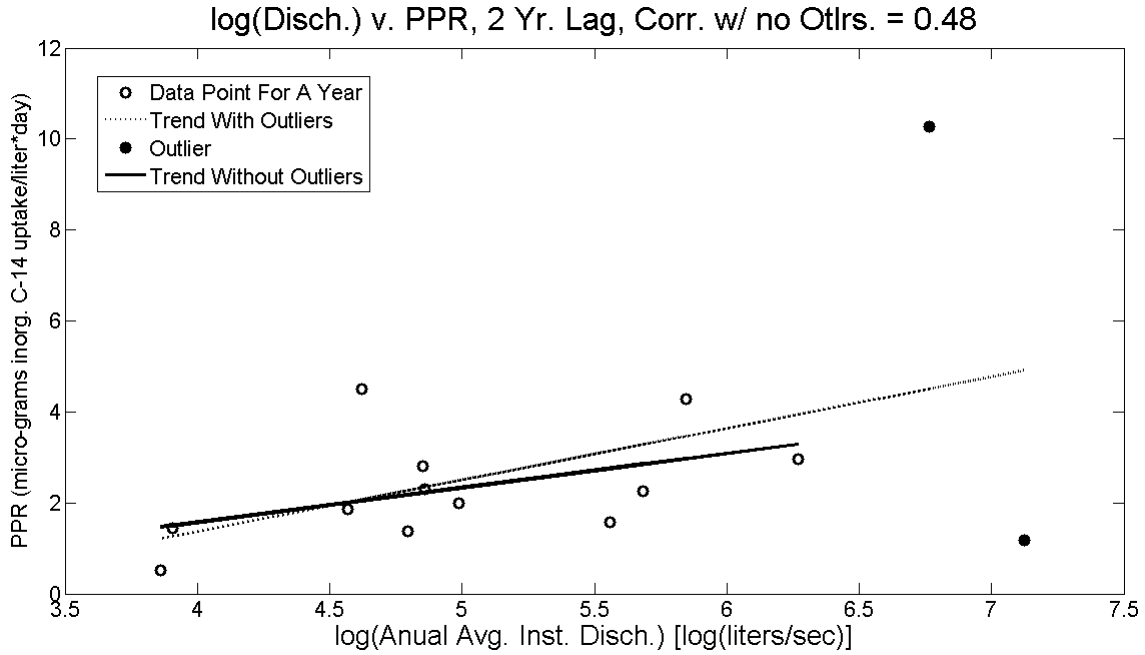

Figure B2c: log(annual average instantaneous discharge) v. primary production, 2 year lag.

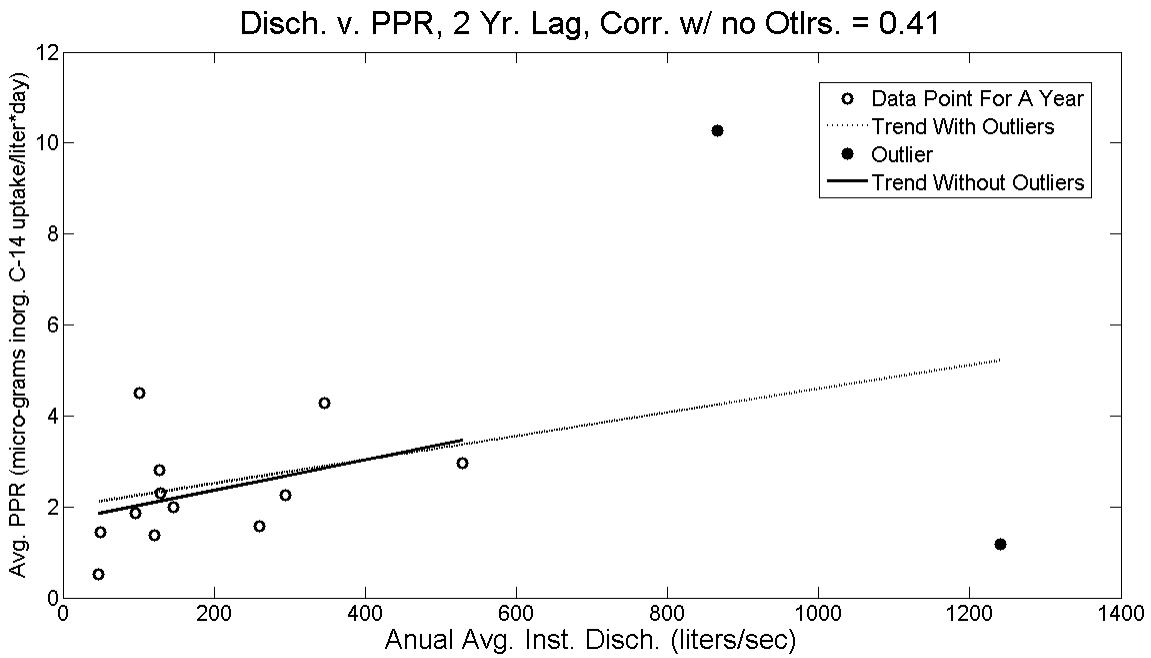

Figure B2d: annual average instantaneous discharge v. primary production, 2 year lag.

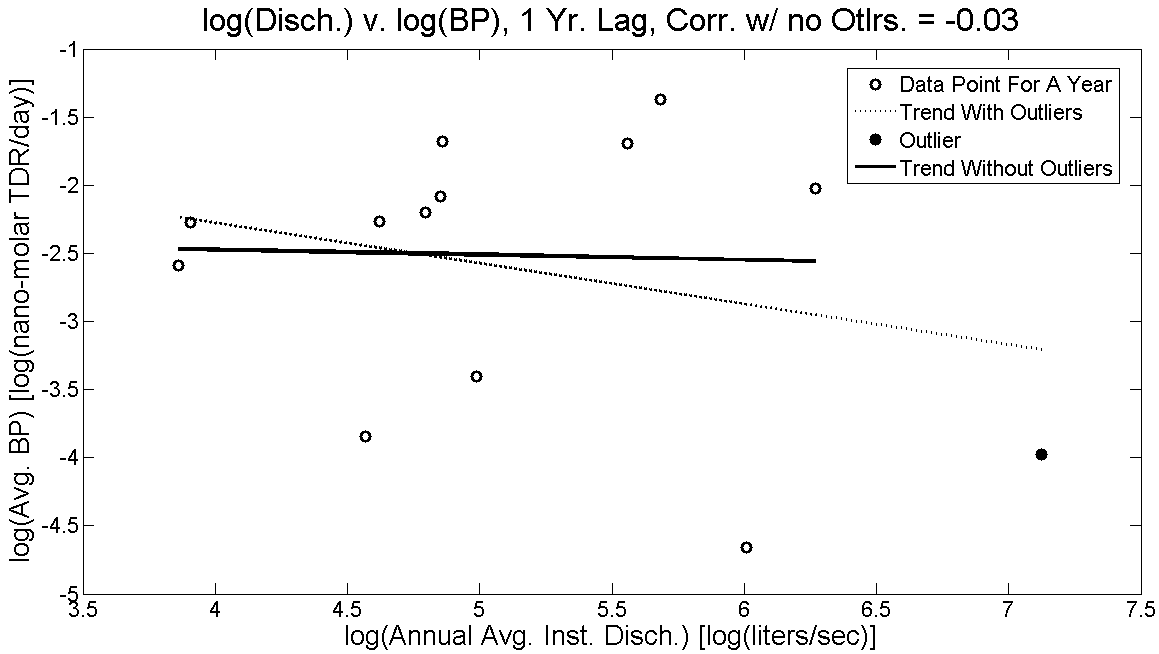

Figure B3a: log(annual average instantaneous discharge) v. log(bacterial production), 1 year lag.

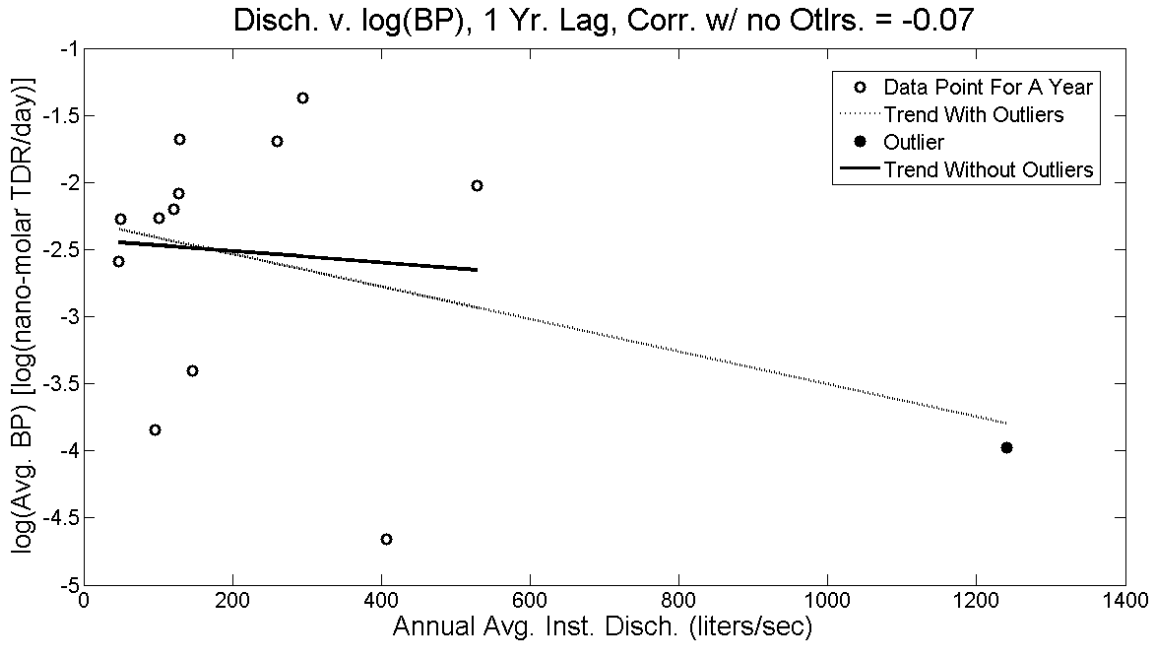

Figure B3b: annual average instantaneous discharge v. log(bacterial production), 1 year lag.

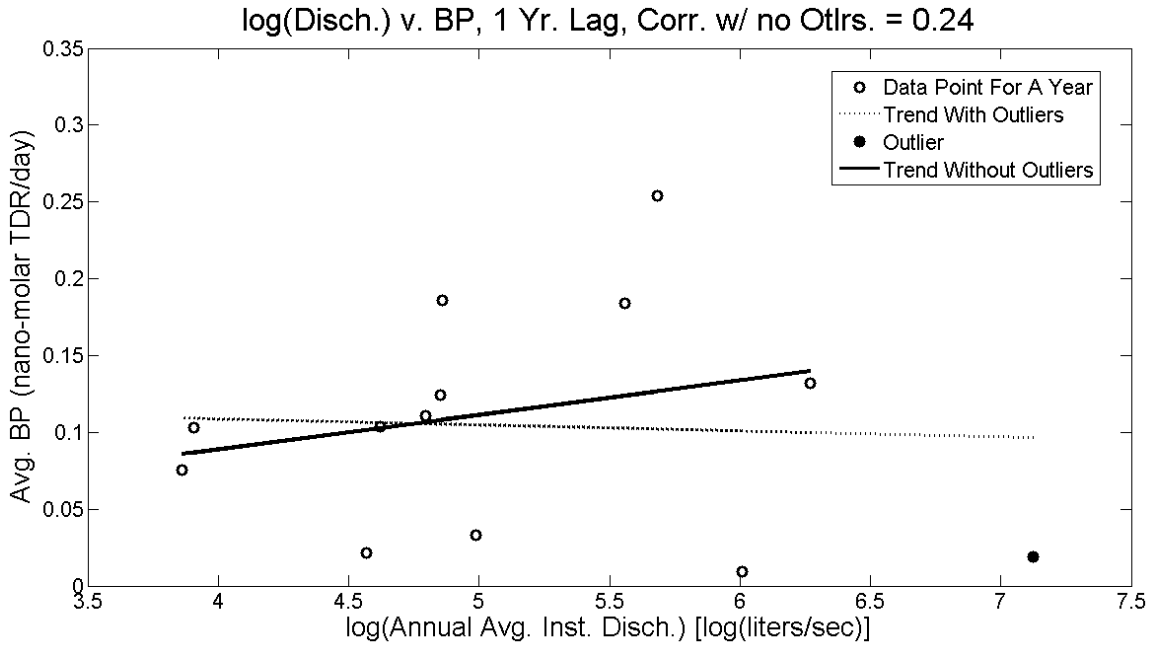

Figure B3c: log(annual average instantaneous discharge) v. bacterial production, 1 year lag.

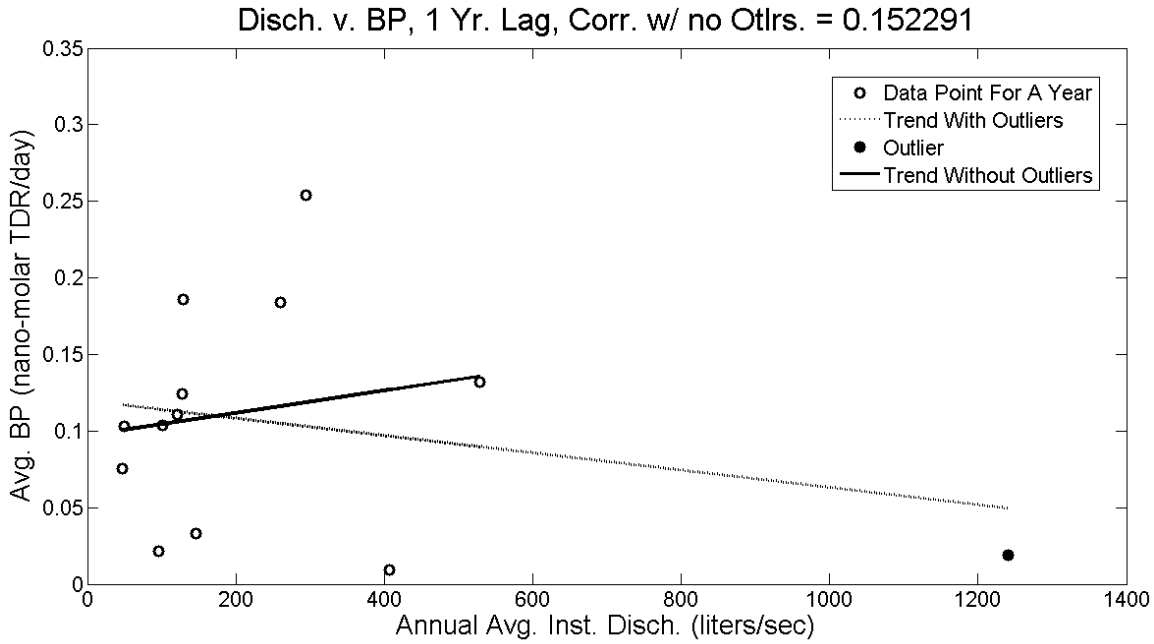

Figure B3d: annual average instantaneous discharge v. bacterial production, 1 year lag.

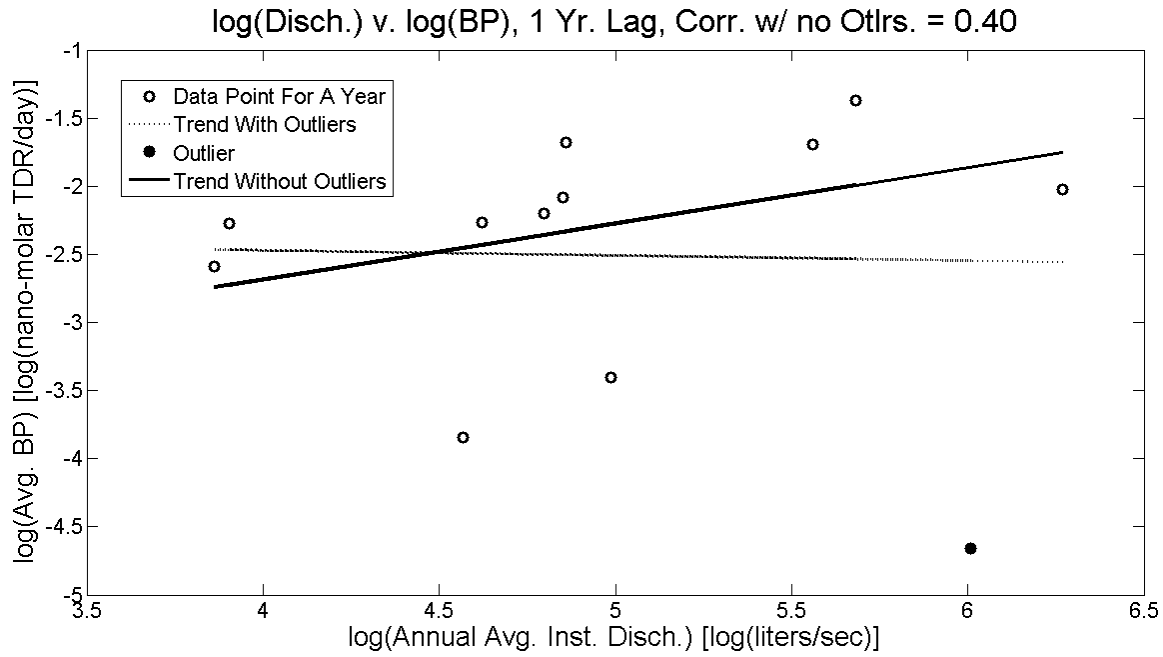

Figure B4a: log(annual average instantaneous discharge) v. log(bacterial production), 1 year lag. Figure B4a is the same as Figure B3a but with the extreme outlier (the 2001 – 2002 flow season) removed. See the "outliers" subsection of the methods section for an explanation.

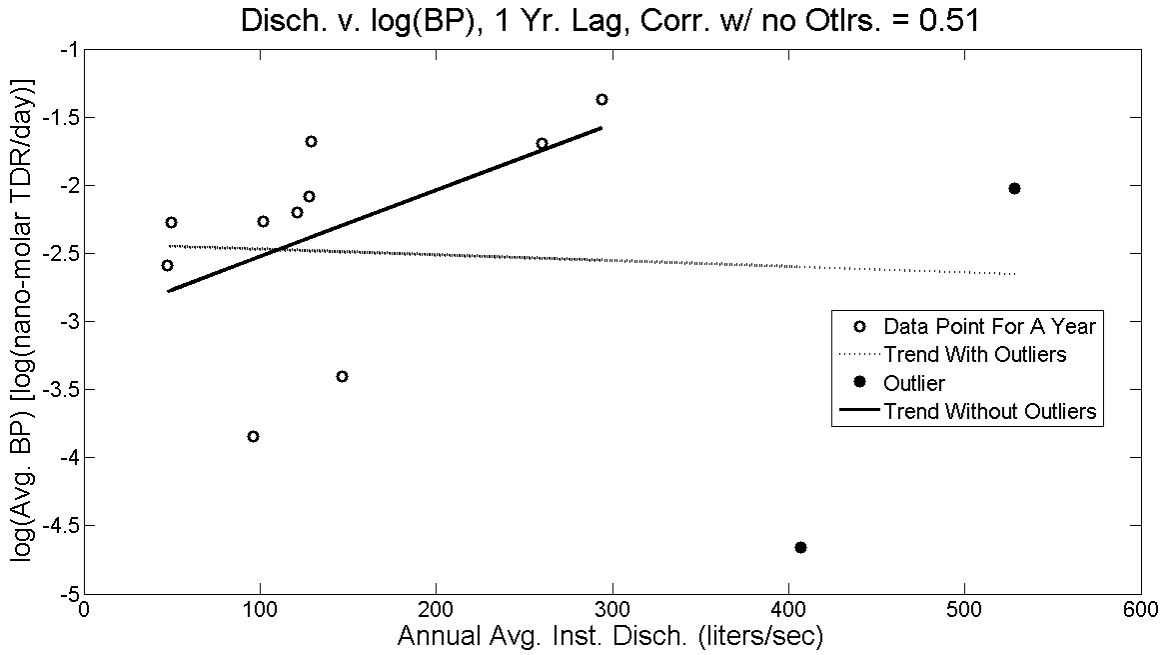

Figure B4b: annual average instantaneous discharge v. log(bacterial production), 1 year lag. Figure B4b is the same as Figure B3b but with the extreme outlier (the 2001 – 2002 flow season) removed. See the "outliers" subsection of the methods section for an explanation.

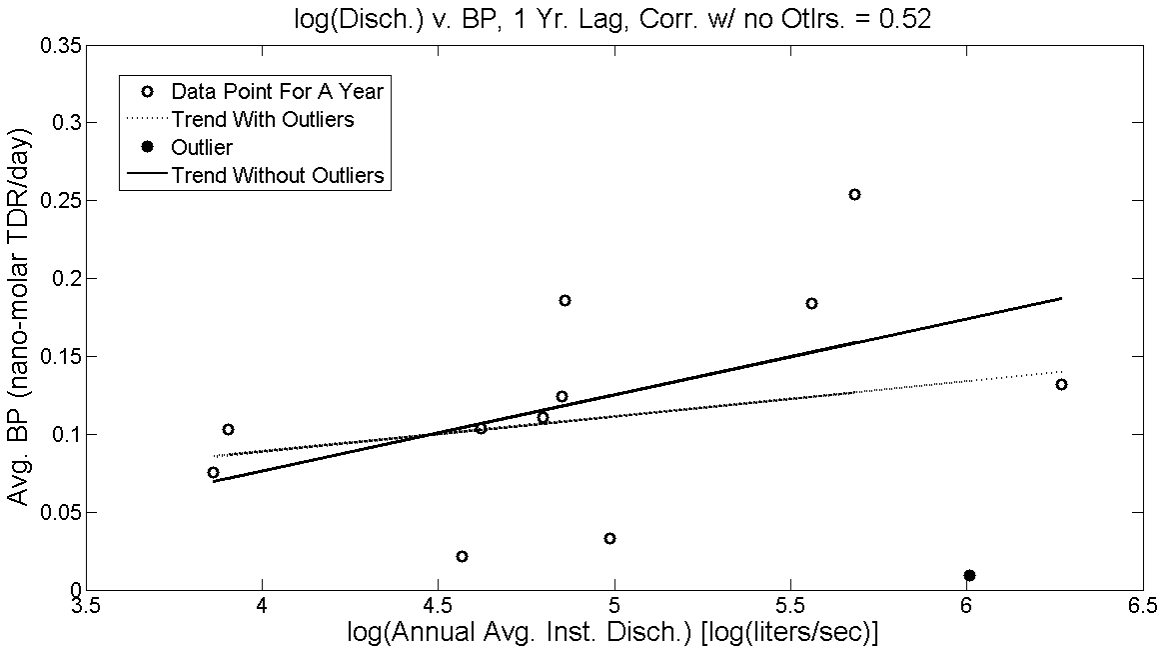

Figure B4c: log(annual average instantaneous discharge) v. bacterial production, 1 year lag. Figure B4c is the same as Figure B3c but with the extreme outlier (the 2001 – 2002 flow season) removed. See the "outliers" subsection of the methods section for an explanation.

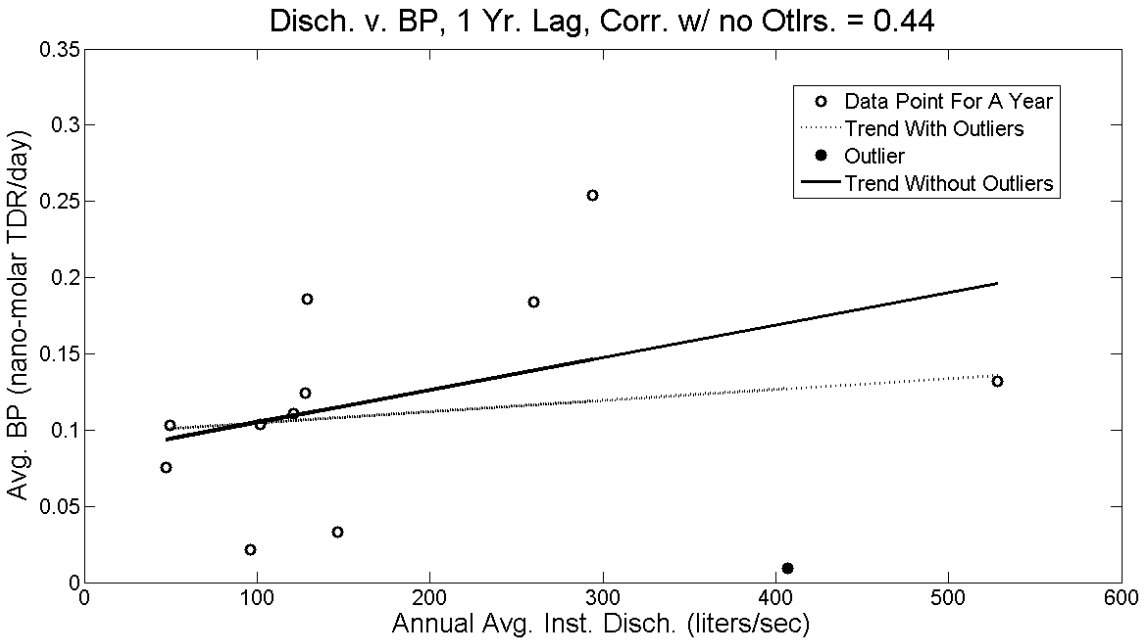

Figure B4d: annual average instantaneous discharge v. bacterial production, 1 year lag. Figure B4d is the same as Figure B3d but with the extreme outlier (the 2001 – 2002 flow season) removed. See the "outliers" subsection of the methods section for an explanation.

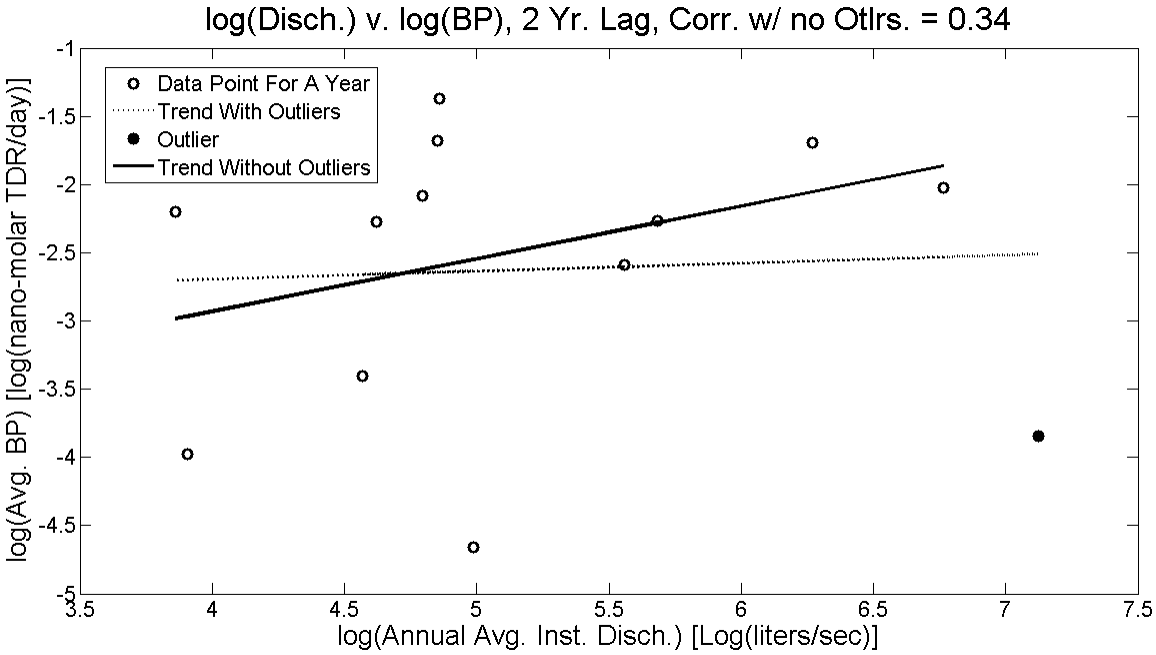

Figure B5a: log(annual average instantaneous discharge) v. log(bacterial production), 2 year lag.

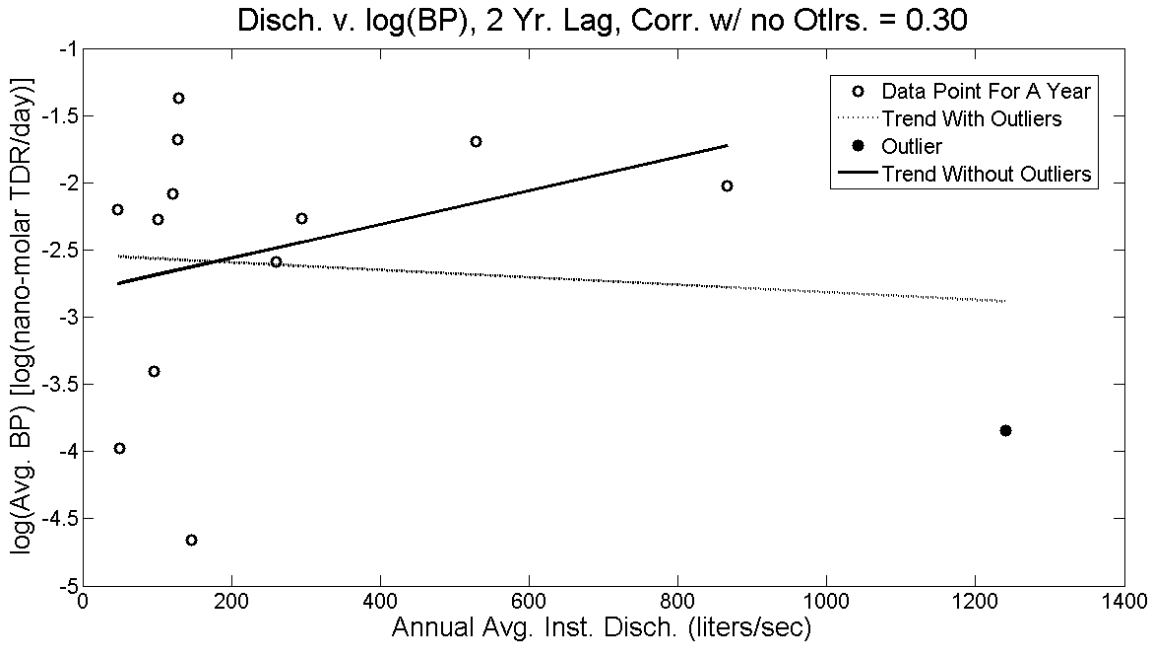

Figure B5b: annual average instantaneous discharge v. log(bacterial production), 2 year lag.

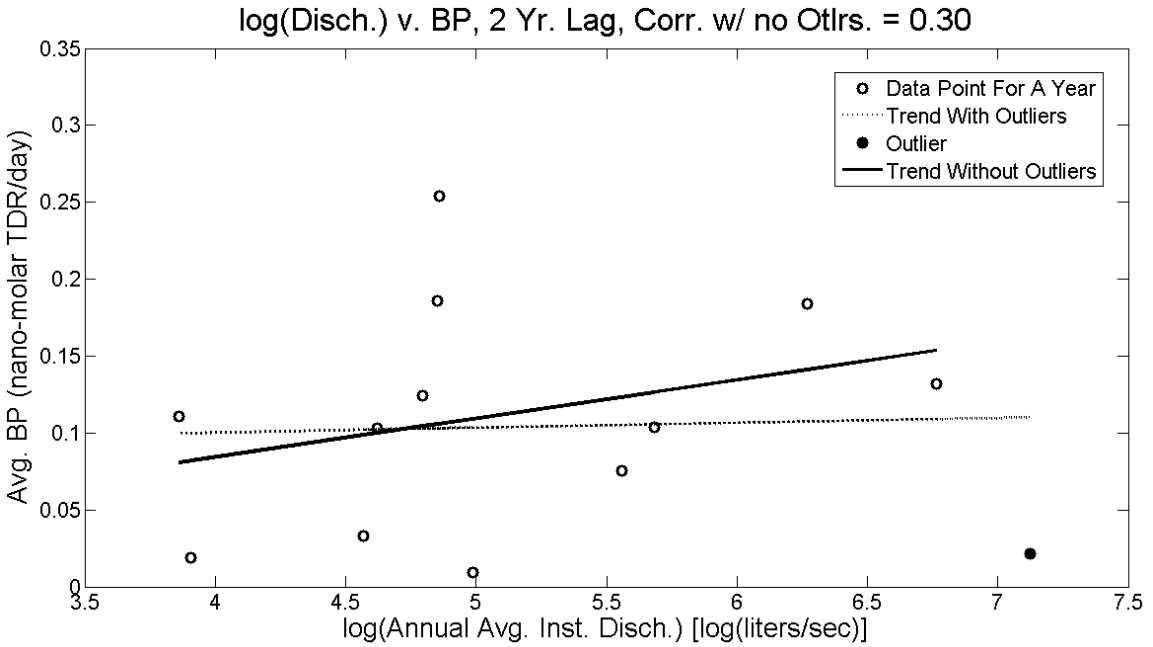

Figure B5c: log(annual average instantaneous discharge) v. bacterial production, 2 year lag.

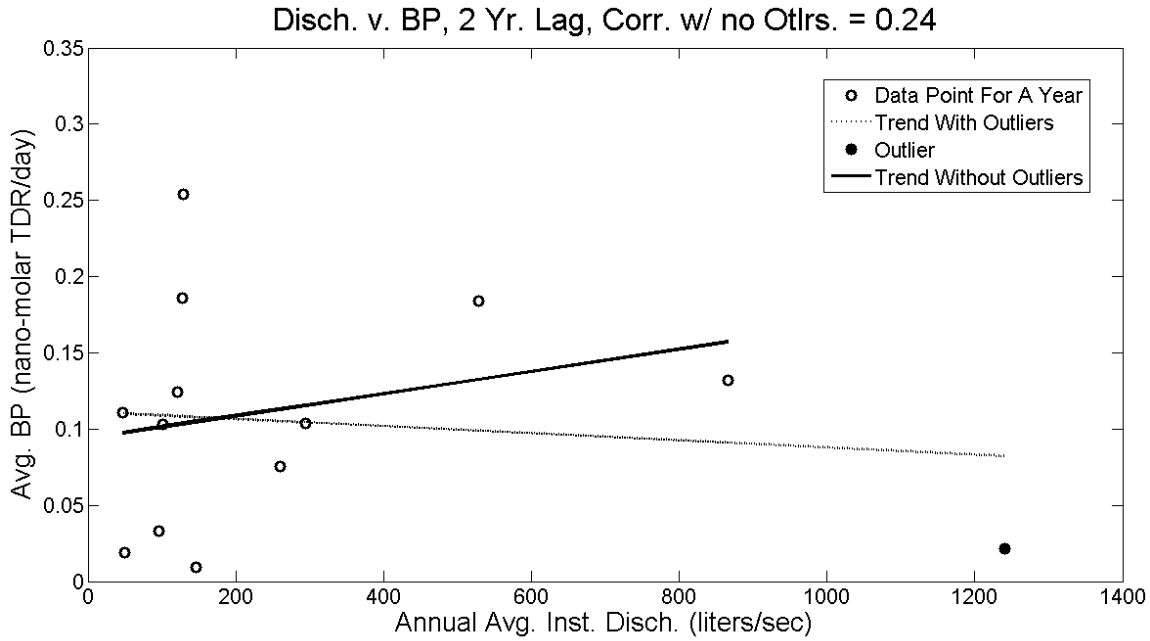

Figure B5d: annual average instantaneous discharge v. bacterial production, 2 year lag.

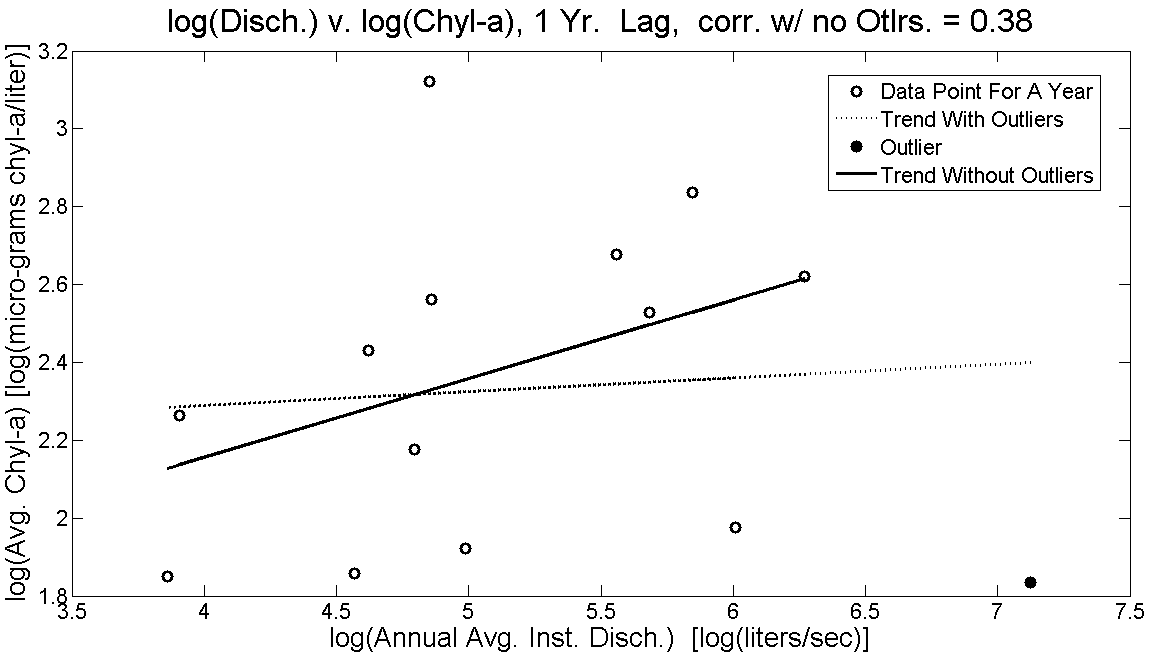

Figure B6a: log(annual average instantaneous discharge) v. log(chlorophyll-a concentration), 1 year lag.

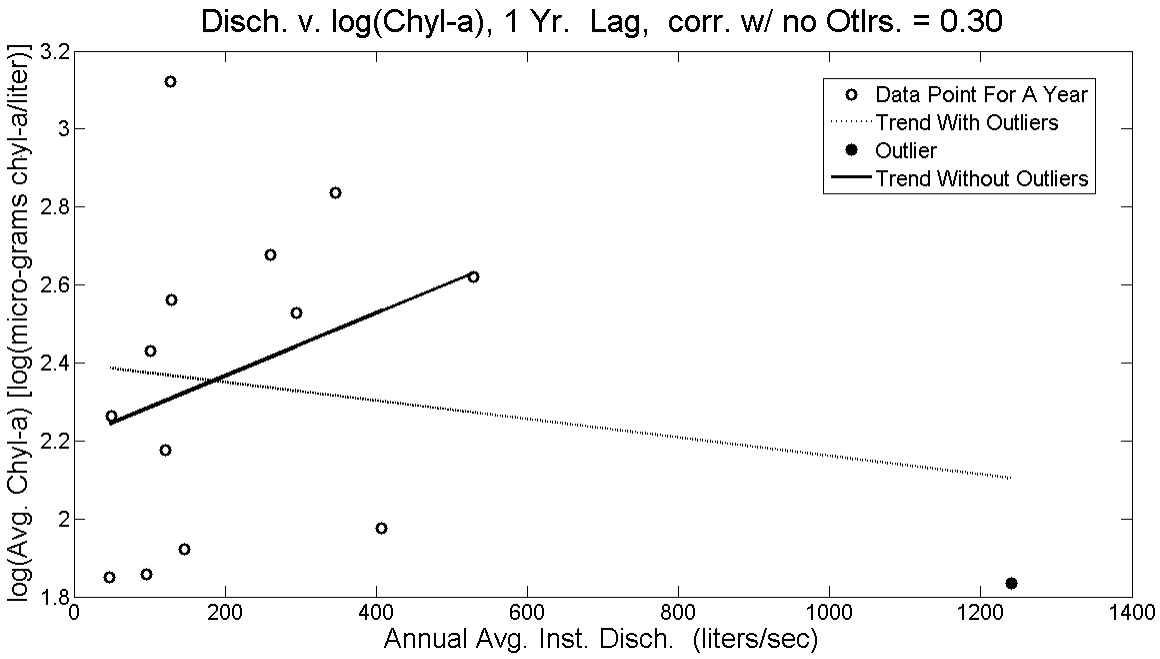

Figure B6b: annual average instantaneous discharge v. log(chlorophyll-a concentration), 1 year lag.

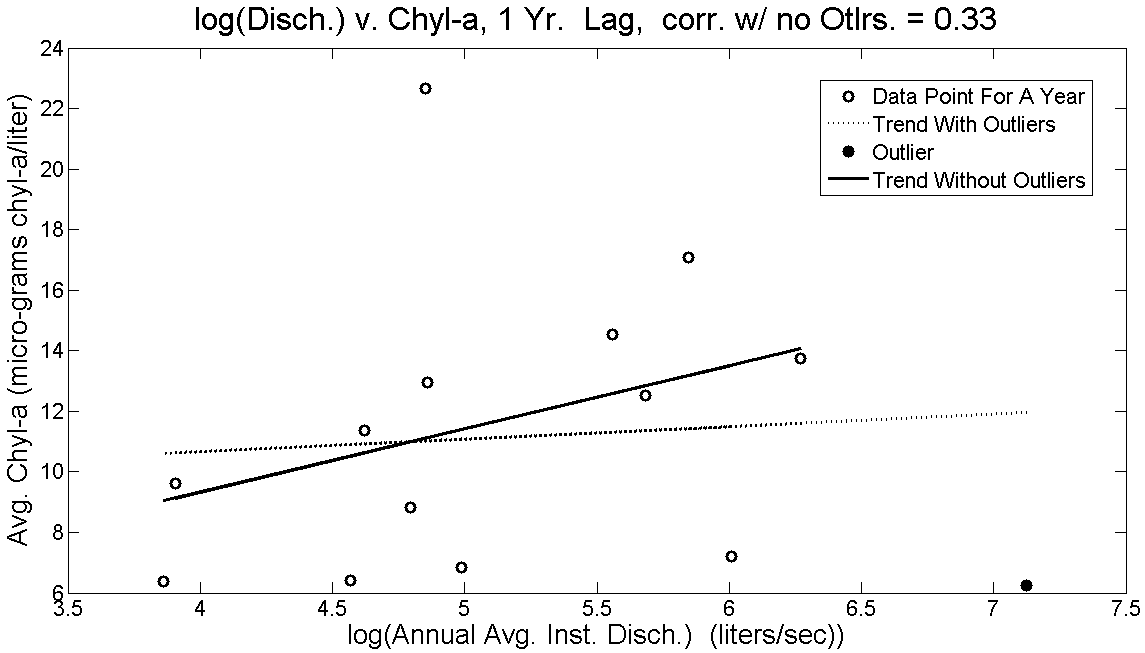

Figure B6c: log(annual average instantaneous discharge) v. chlorophyll-a concentration, 1 year lag.

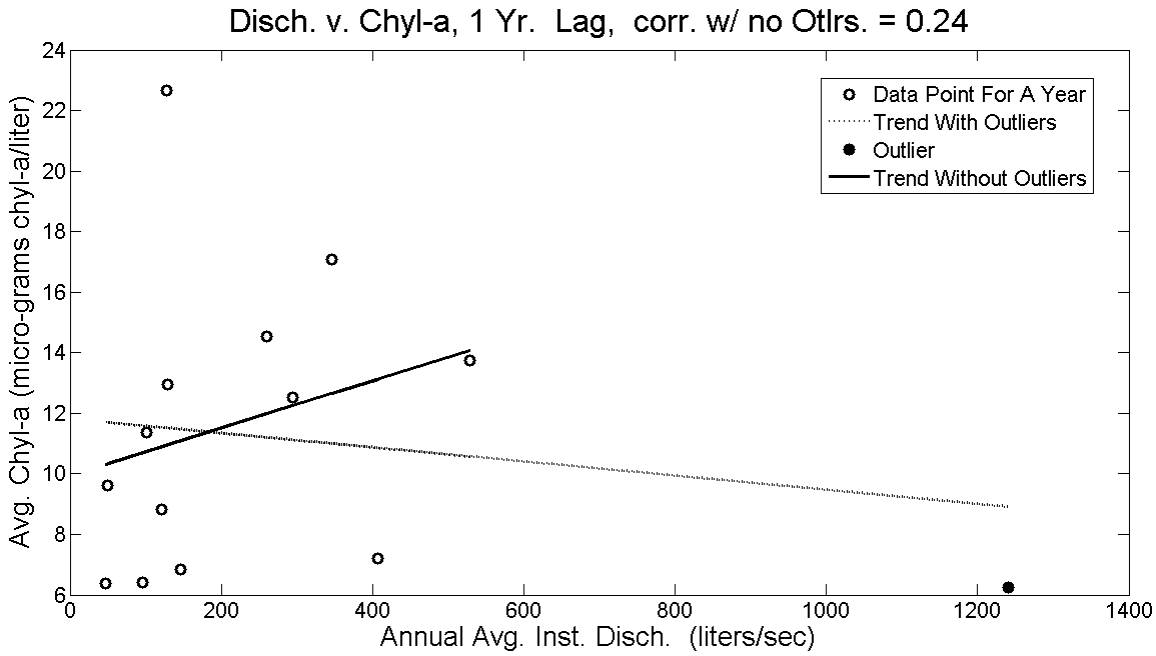

Figure B6d: annual average instantaneous discharge v. chlorophyll-a concentration, 1 year lag.

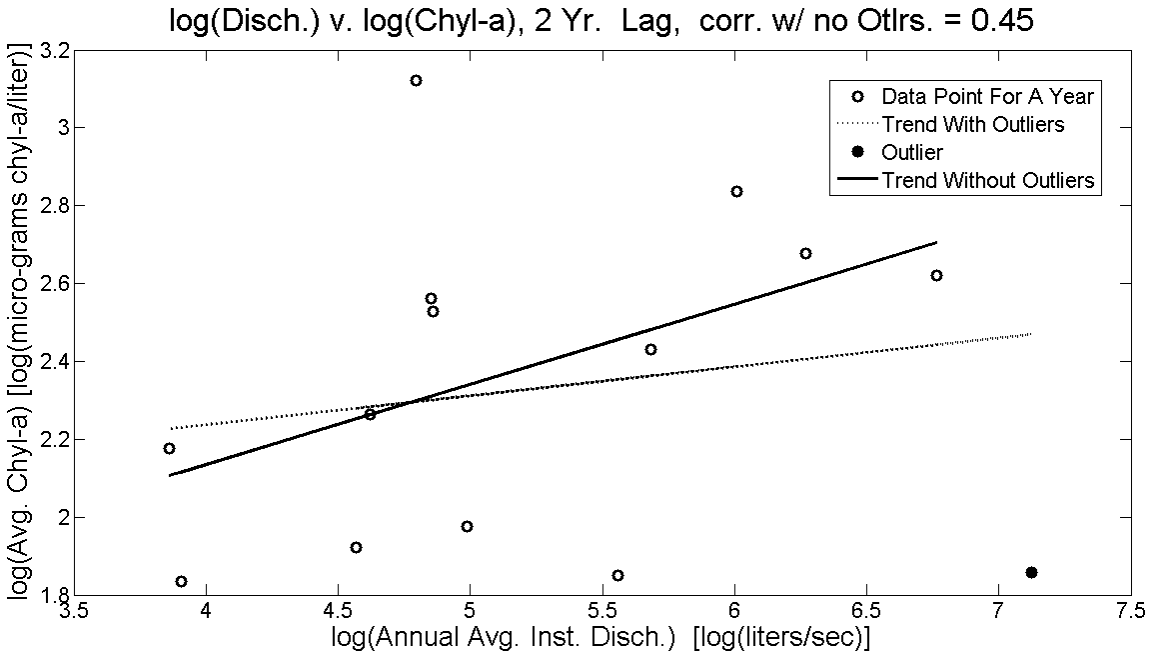

Figure B7a: log(annual average instantaneous discharge) v. log(chlorophyll-a concentration), 2 year lag.

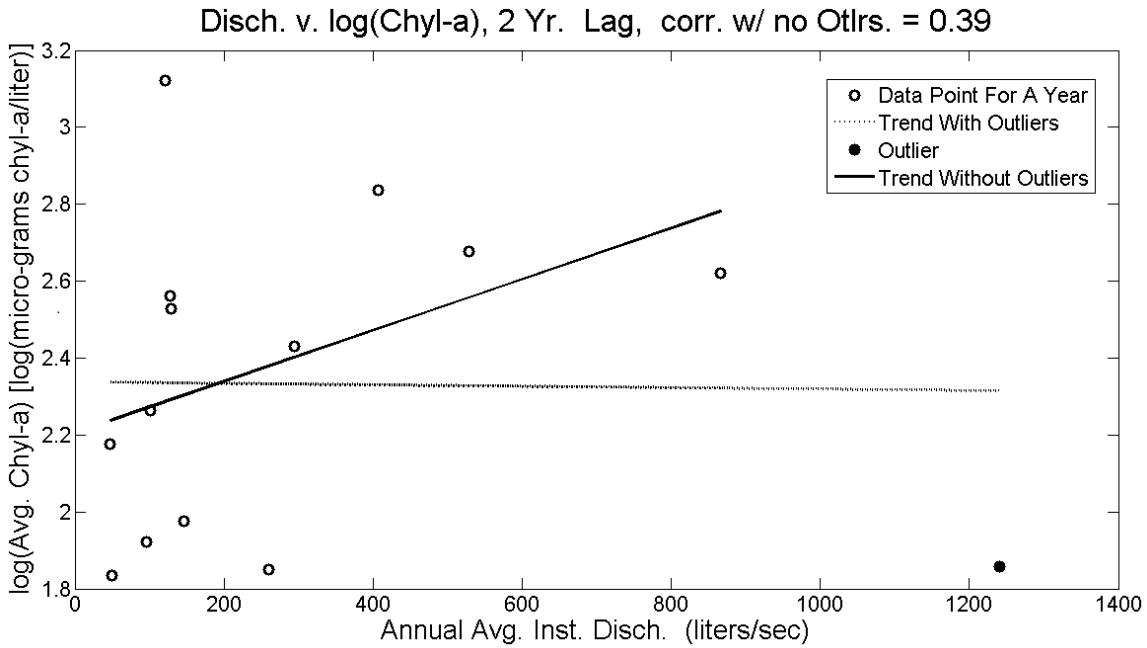

Figure B7b: annual average instantaneous discharge v. log(chlorophyll-a concentration), 2 year lag.

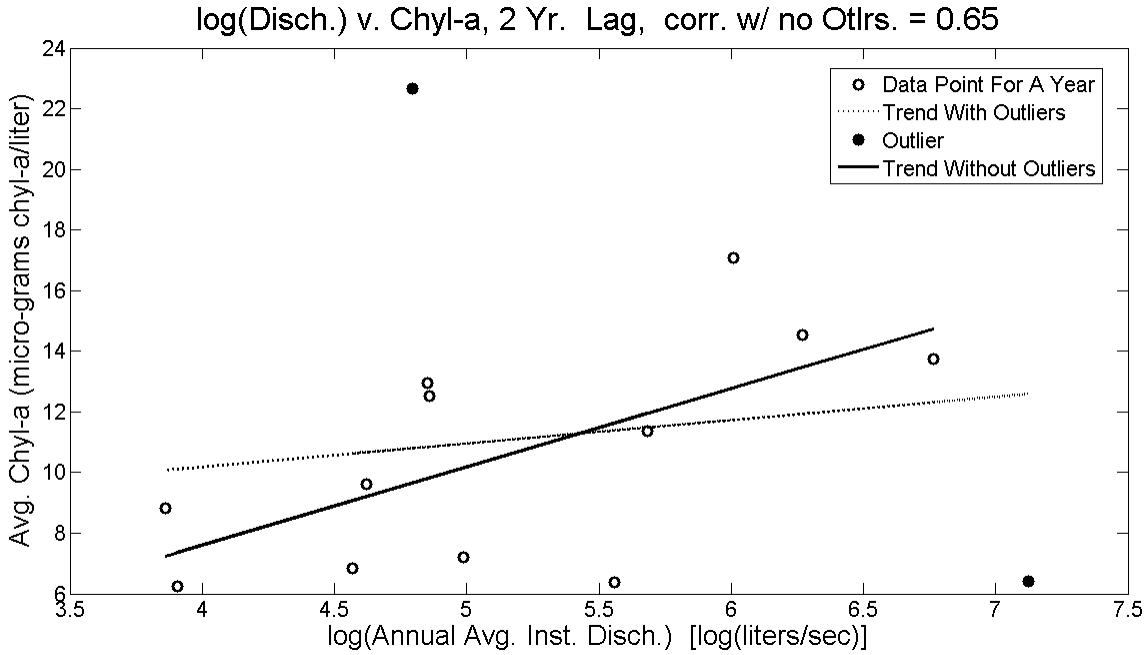

Figure B7c: log(annual average instantaneous discharge) v. chlorophyll-a concentration, 2 year lag.

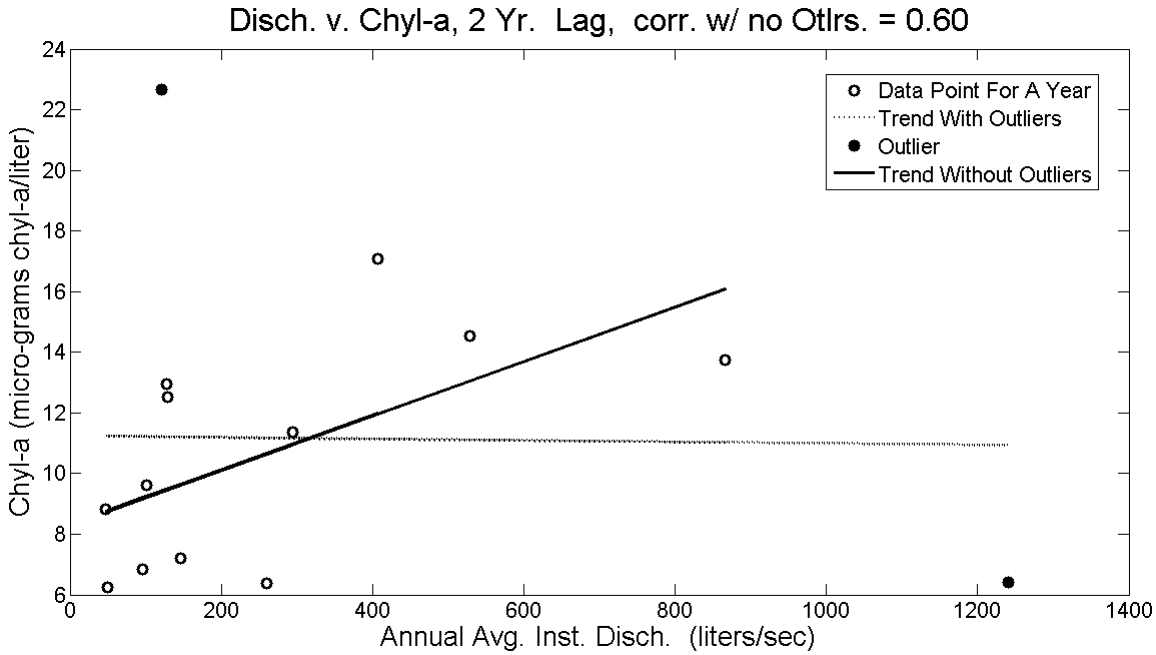

Figure B7d: annual average instantaneous discharge v. chlorophyll-a concentration, 2 year lag.

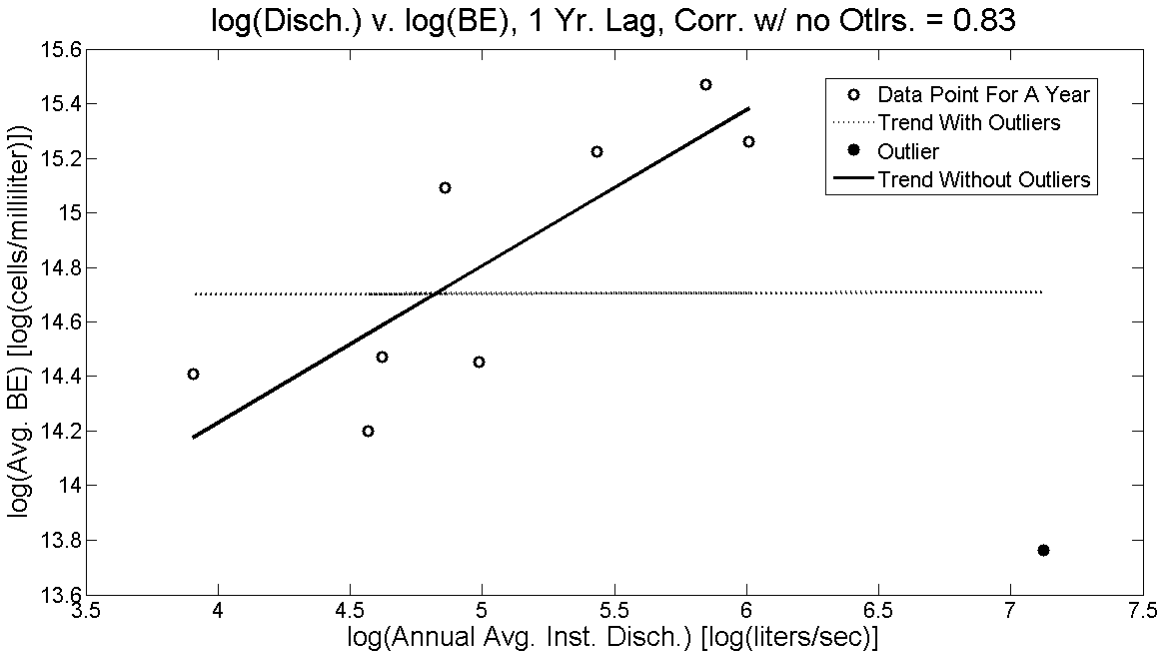

Figure B8a: log(average instantaneous discharge) v. log(bacterial enumeration), 1 year lag.

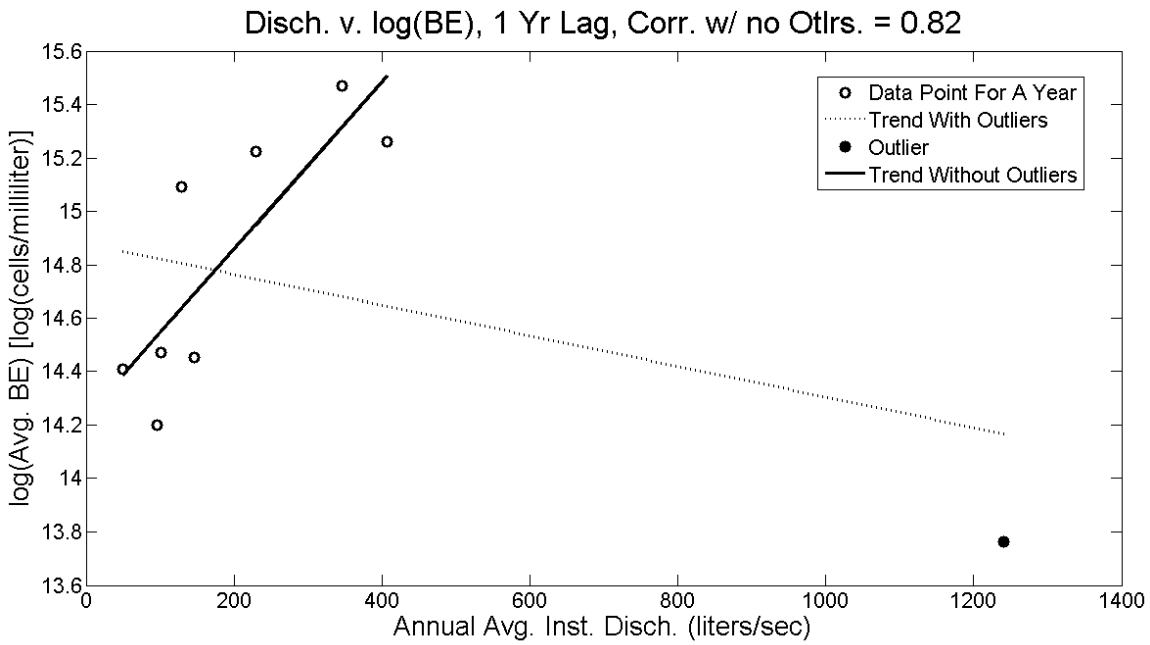

Figure B8b: average instantaneous discharge v. log(bacterial enumeration), 1 year lag.

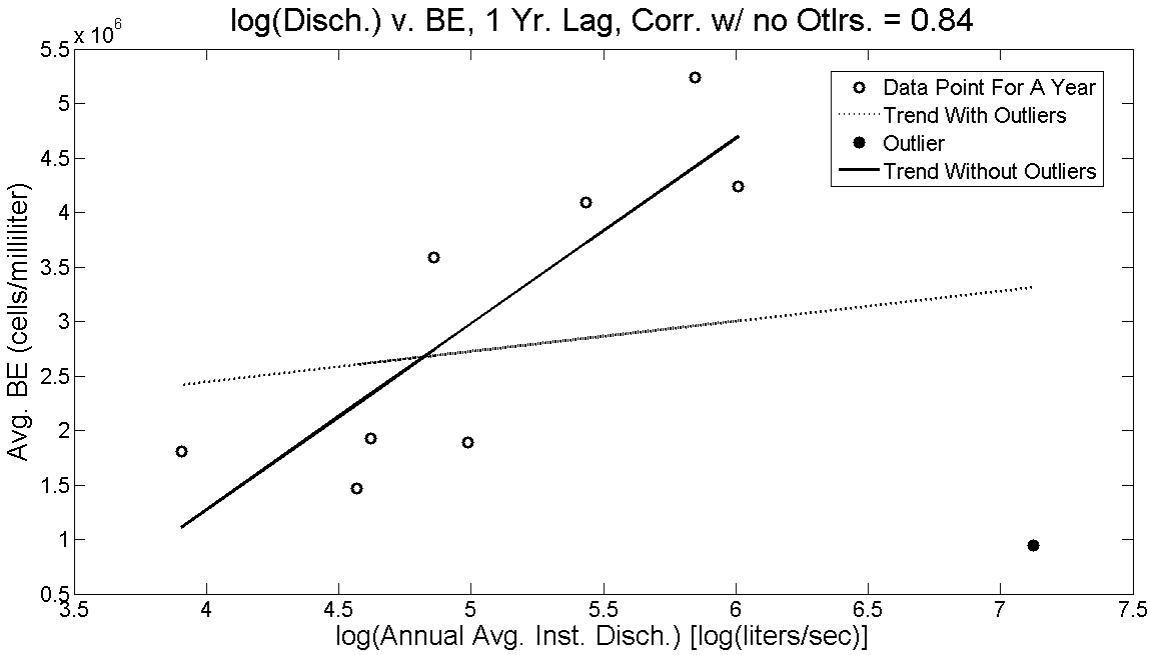

Figure B8c: log(average instantaneous discharge) v. bacterial enumeration, 1 year lag.

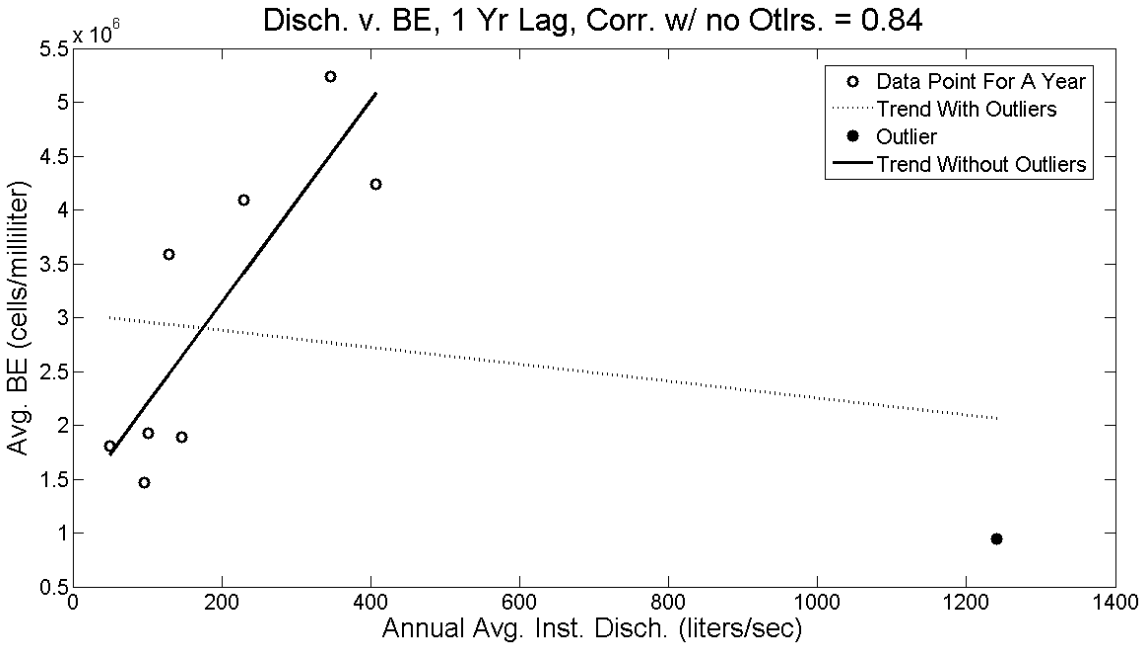

Figure B8d: average instantaneous discharge v. bacterial enumeration, 1 year lag.

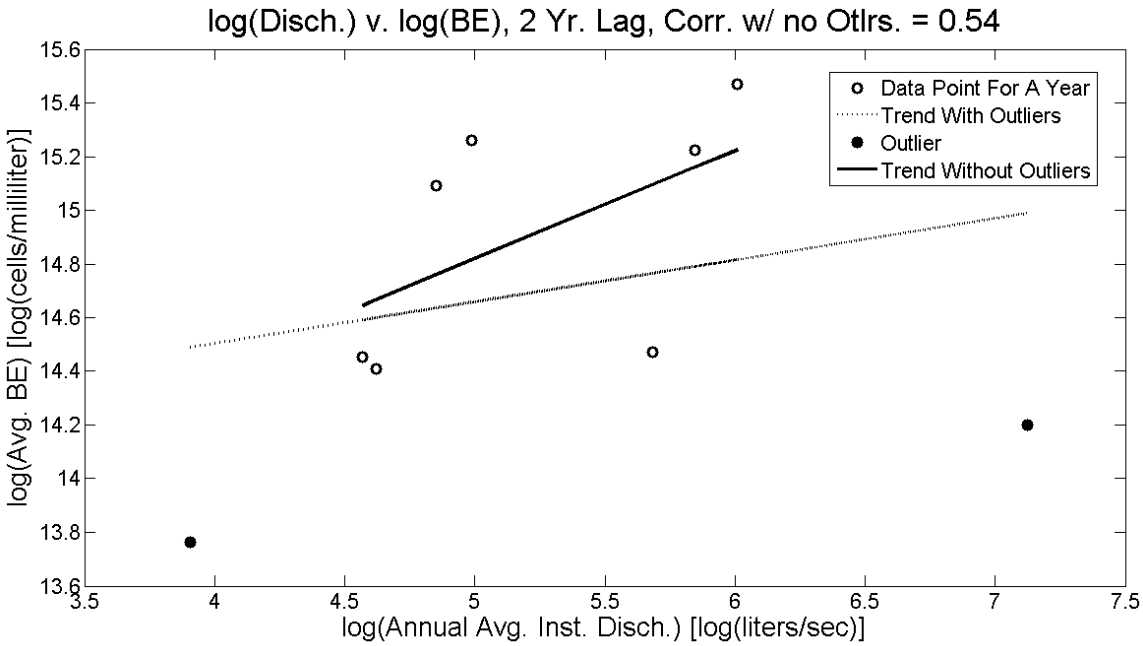

Figure B9a: log(average instantaneous discharge) v. log(bacterial enumeration), 2 year lag.

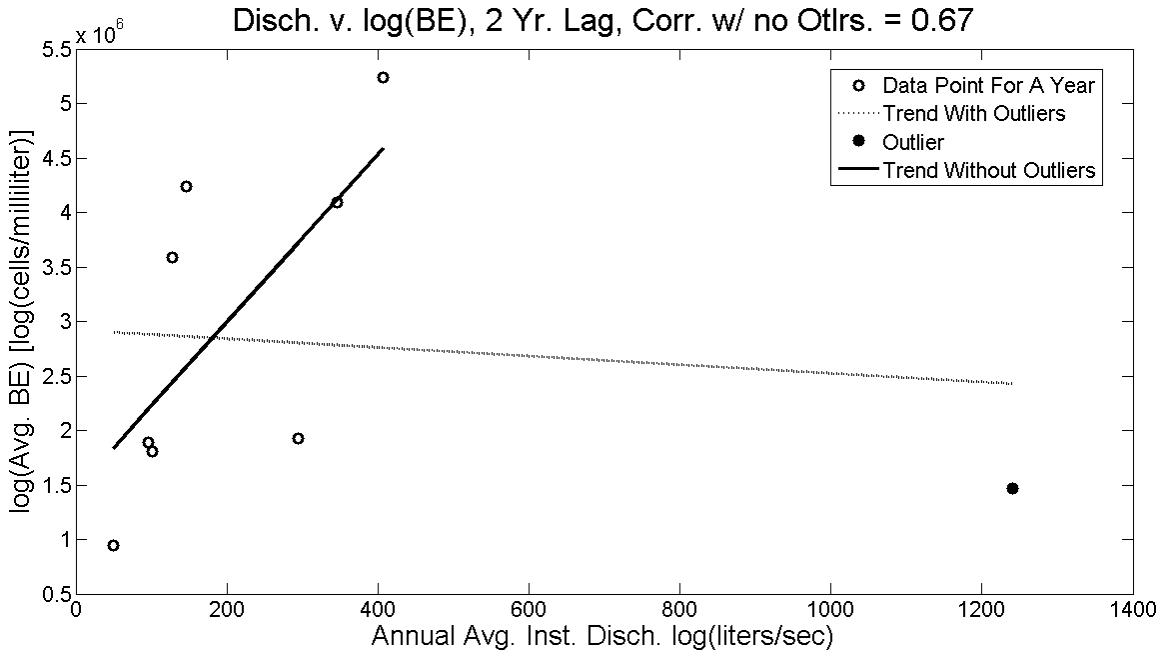

Figure B9b: average instantaneous discharge v. log(bacterial enumeration), 2 year lag.

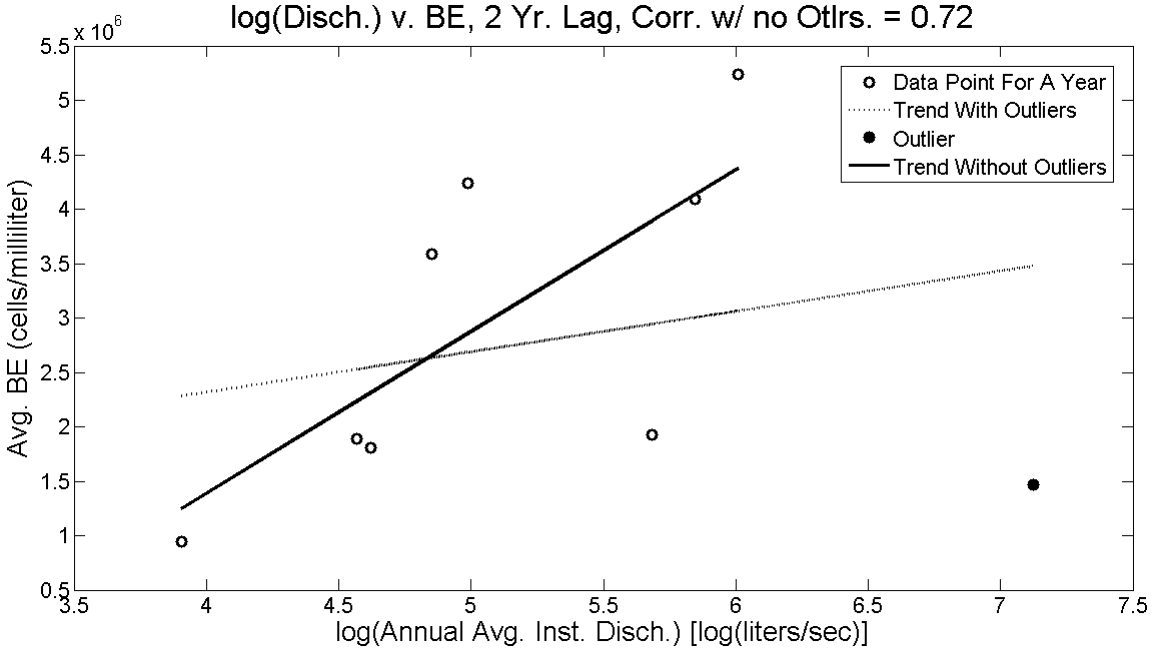

Figure B9c: log(average instantaneous discharge) v. bacterial enumeration, 2 year lag.

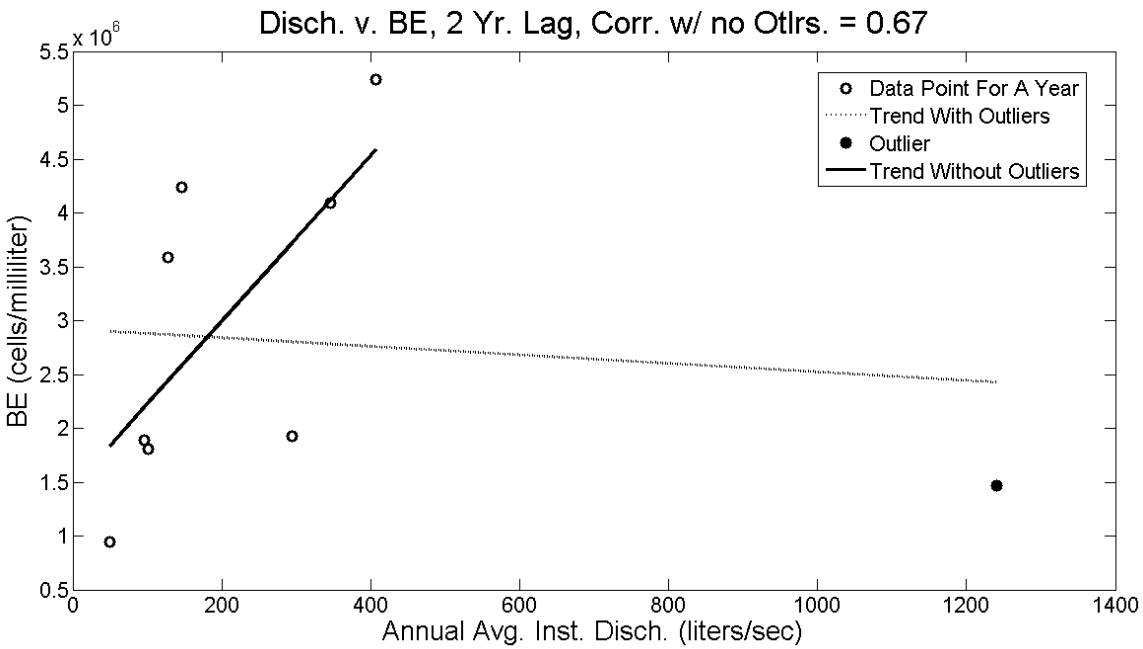

Figure B9d: average instantaneous discharge v. bacterial enumeration, 2 year lag.